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INTERMOUNTAIN BIOGEOGRAPHY: A SYMPOSIUM



GREAT BASIN NATURALIST MEMOIRS

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K. T. Harper
and
James L. Reveal
Symposium Organizers



CONTENTS

	Page
Preface	1
The biota of the Intermountain Region in geohistorical context. Arthur Cronquist	3
Biogeography of intermountain fishes. Gerald R. Smith	17
Zoogeography of reptiles and amphibians in the Intermountain Region. Wilmer W. Tanner	43
Avian biogeography of the Great Basin and Intermountain Region. William H. Behle	55
The flora of Great Basin mountain ranges: Diversity, sources, and dispersal ecology. K. T. Harper, D. C. Freeman, W. K. Ostler and L. G. Klikoff	81
Alpine phytogeography across the Great Basin. W. D. Billings	105
Phytogeographical variation within juniper-pinyon woodlands of the Great Basin. Neil E. West, Robin J. Tausch, Kenneth H. Rea, and Paul T. Tueller	119
Patterns of avian geography and speciation in the Intermountain Region. Ned K. Johnson	137
Explosive evolution of perennial <i>Atriplex</i> in western America. Howard C. Stutz	161
Distribution and phylogeny of Eriogonoideae (Polygonaceae). James L. Reveal	169
Problems in plant endemism on the Colorado Plateau. Stanley L. Welsh	191
Some factors governing plant distributions in the Mojave-Intermountain Transition Zone. Susan E. Meyer	197
The theory of insular biogeography and the distribution of boreal birds and mammals. James H. Brown	209
Biogeography and management of native western shrubs: A case study, Section <i>Tridentatae</i> of <i>Artemisia</i> . E. Durant McArthur and A. Perry Plummer	229
Applying biogeographic principles to resource management: A case study evaluating Holdridge's Life Zone model. James A. MacMahon and Thomas F. Wieboldt ...	245
Index	259

Intermountain Biogeography: A Symposium

No. 2

Brigham Young University, Provo, Utah

1978

K. T. Harper¹ and James L. Reveal²

PREFACE

Most of the Intermountain Region is remote from the nation's major transportation arterials. As a consequence, the region's beauty and its biological resources are largely unappreciated. The area is often considered to be a wasteland, a desert with little or no life, and a land of minimal value. Because few initially understood or appreciated the region, its resources have often been abused by a variety of human activities ranging from military weapon testing to off-road vehicle travel. Additionally, ranchers and governmental land managers have had no precedents to guide their activities in the unique and often fragile ecosystems of the region. As a consequence, the biological landscape has been markedly altered by grazing, control of wildfires, and agronomic practices. With time and knowledge, concern for the natural landscape of the West has grown. National and state legislation now imposes strict guidelines on most new development activities and requires a balanced analysis of the full impact of major activities on the land. Even rare native species have advocates in high places and now enjoy some legal protection.

Although knowledge has accumulated and management of the biological resources of the region has steadily improved, there is still much to do. New facts must be accumulated and those now known must be digested, disseminated, and put to work in management by individuals and governments. This volume brings together current information on a broad spectrum of the native biota of the region. Most of the authors consider the management implications of their findings. We hope the volume will inform and assist resource managers charged with preserving the ecological health of the Intermountain West.

For the biologist, this book presents the first major overview of current biogeographical research being conducted by a number of individuals and institutions in the intermountain region. Of more importance, however, this symposium represents the first attempt to bring both plant and animal scientists and management-oriented researchers together to discuss and evaluate the biogeographic principles at work in the area. Topics discussed include distribution patterns for fishes, reptiles, amphibians, birds,

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small mammals, and plants within the intermountain region. Special reviews are presented on *Artemisia*, *Atriplex*, and the genus *Eriogonum* and its relatives. Several broad biological problem areas within the region are reviewed, including the nature of the floristic transition zone between the Mojave and Great Basin deserts, the endemic flora of the Colorado Plateau, the distribution of the juniper-pinyon community in the Great Basin, and the evolutionary development of the alpine biota of the Intermountain Region. Special considerations are given to the problems of managing native plant and animal populations in the area.

The general public will be especially interested in the role biogeographic considerations are now playing in the understanding of the present-day distribution of organisms within the Intermountain Region and the management options available for the use and protection of these vital natural resources. Public land managers will find that many of the biogeographic principles discussed will help them to better understand the nature of arid land resources, endangered species, and the impact of man's technology in the American West.

Each chapter stands as a unit with an introduction, a discussion, and a summary of pertinent literature. An index completes the volume.

The Intermountain Biogeography Symposium was held at the University of Montana, Missoula, 14-15 June 1976. The symposium was sponsored by Brigham Young University and the Intermountain Forest and Range Experiment Station of the U.S. Forest Service, with the cooperation of the Botanical Society of America and the Pacific Section of the American Association for the Advancement of Sciences. The symposium was arranged by Kimball T. Harper of Brigham Young University and Ralph C. Holmgren of the U.S. Forest Service, with the assistance of Dr. George Edmunds of the University of Utah, Dr. Joseph Murphy of Brigham Young University, Dr. Neil West of Utah State University, and Edward Smith of the Bureau of Land Management. Major financial support for the symposium and the publication of these proceedings has been provided by Brigham Young University and the U.S. Forest Service. We thank Dr. Stephen L. Wood, editor of the *Memoirs* series of the *Great Basin Naturalist* and the staff of Brigham Young University Press for their help in bringing the book to publication. The cover was designed by Kaye H. Thorne.

K. T. Harper
and
J. L. Reveal
Symposium Organizers.

THE BIOTA OF THE INTERMOUNTAIN REGION IN GEOHISTORICAL CONTEXT

Arthur Cronquist¹

ABSTRACT.—The present Great Basin Floristic Province had achieved roughly its present topographic conformation by some time in the Miocene epoch and had a climate not too different from the present one, though probably a little warmer, moister, and less continental. Both the flora and the fauna took on a fairly modern aspect during the Miocene, as a result of worldwide evolutionary changes and more specific adaptation to the conditions of the region. Changes in the biota since that time mainly reflect evolution and migration at the level of species and, to a lesser extent, genera, in response to regional conditions and the repeated fluctuations in climate. The climatic reversals of the Pleistocene caused repeated inverse migrations of more northern, mesophytic elements in the flora, on the one hand, and more southern, xerophytic elements on the other. These expansions and contractions of range favored hybridization and genetic mixing among related plant species. The fauna of the region, dependent eventually on the flora, must have been subjected to basically the same set of repeated changes in range and local distribution during the Pleistocene. About 10,000 years ago many of the large mammals in the Intermountain Region, as elsewhere in North America, rapidly became extinct, perhaps largely through overkill by primitive man.

A proper understanding of the present is always facilitated by some knowledge of the past. Therefore I want to say something about the geological and biological history of the Intermountain Region, to help provide a proper setting for the other papers of this symposium. Nearly everything that I have to say is already in the scientific literature somewhere, but the particular synthesis may be in part new.

As a first approximation of the truth, one may say that the aspect of the vegetation of any region is controlled by the climate, and the taxonomic composition of the flora is determined by the climate and the history. The general nature of the fauna is in turn determined by the vegetation, and the taxonomic composition of the fauna is determined by the vegetation and the history.

It is, of course, also true that the fauna influences the flora. One of the reasons that grasses predominate in certain climates is that they are better adapted to withstand grazing than are most other herbaceous plants. Furthermore, evolution of floral structure is to some extent correlated with

the evolution of pollinating insects (Leppik 1957), and particular species of plants may become dependent on particular pollinators. A notable example that may be familiar to many readers is provided by *Yucca* and the *Tegeticula* moth. Some of the importance of the influence of the fauna on the flora is also shown by the devastating effect of the introduction of goats to some of the islands off the Pacific Coast of southern North America. More complex interactions between plants and animals also occur. Yet the preponderant control is that exerted by the food makers (plants) on the food eaters (animals). Therefore it is reasonably possible to consider the vegetation and flora of a region with only secondary attention to the fauna, whereas any proper consideration of the fauna must be grounded in a knowledge of the vegetation. These facts, or what I take to be facts, are fortunate for me, because I know a lot more about plants than I do about animals.

The Intermountain Region may be variously delimited. For purposes of this discussion, I take its limits to be those of the

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Great Basin Floristic Province, as defined by Gleason and Cronquist (1964). In large part these limits are the same as those of the Intermountain Flora (Cronquist et al. 1972), but the Great Basin Floristic Province extends somewhat further south into Arizona and also includes a part of northwestern New Mexico as well as a sliver of western Colorado. In addition to the hydrographic Great Basin, the area under consideration also includes the Snake River Plain and the more westerly segment of the Colorado Plateau. The region has a continental climate, with fairly hot, dry summers, and cold, snowy winters. The lowlands and foothills are largely desert and semidesert; a more mesophytic flora often occupies the upper elevations. South of the Intermountain Region lie hotter deserts, marked especially by milder winters. These southern deserts have a rather different flora, and the plant communities are often dominated by *Larrea*. The southern deserts are not a part of the Intermountain Region as here defined.

GEOLOGIC HISTORY

We shall start our consideration of the intermountain biota with a summary of the geologic history of the region from the Cretaceous period to the present. Much of the information in this section comes from papers by Bateman (1968), Eardley (1968), and Roberts (1968).

The present Intermountain Region has been at middle latitudes since before the beginning of the Cretaceous. North America has drifted westward, with respect to Europe and Africa, throughout that time, but the latitude of our area has changed relatively little (Dietz and Holden 1970, Smith et al. 1973).

Our region has been subjected to repeated and almost continuous tectonic disturbance, leading to uplift and erosion, from the beginning of the Cretaceous to the present. The terrain throughout that time has been highly varied, doubtless producing a

diversity of habitats. The Upper Cretaceous, in particular, was a time of great and prolonged uplift in western Utah and eastern Nevada. There was a large interior drainage basin in north-central Nevada even in the late Upper Cretaceous, and in mid-Eocene time there appear to have been high mountains and large lake basins throughout most of the present hydrographic Great Basin. In Oligocene time these lake basins were considerably elevated and themselves subjected to erosion.

The present Rocky Mountains and Colorado Plateau began to rise early in the Tertiary, and they have continued to rise at varying rates until the present. The Sierra Nevada, bounding the Great Basin on the west, also has a long history. After a relative quiescence during the Oligocene, the tilt-uplift of the Sierra Nevada was considerably accentuated during the Miocene. The concurrent uplift of the Rocky Mountains and Colorado Plateau shaped the Great Basin. By some time in the Miocene, it appears that "basin and range topography extended from the Wasatch Mountains to the Sierra Nevada, and most of the area drained into interior basins" (Roberts 1968). There is some difference of opinion on the timing, however, and Axelrod (1950) believes that the present interior drainage of the Great Basin dates from near the close of the Pliocene.

The Snake River Plain, forming a broad crescent across southern Idaho, belongs to the Great Basin floristic province but is geologically distinctive. The Upper Cretaceous uplift in western Nevada and eastern Utah extended across the present Snake River Plain as well. During Eocene time the present Snake River Plain was buried by lava in a major and prolonged tectonic disturbance that formed a volcanic plateau extending from western Wyoming across southern Idaho and probably into eastern Oregon. In Oligocene time the Snake River basin took shape, possibly "as a tension rift in the lee of the Idaho batholith" (Axelrod 1968), which began to drift north. Sub-

sidence of the basin and outpouring of new lava flows have continued until the present time. The youngest deposits in the Craters of the Moon region at the north edge of the Snake River Plain are probably only a few hundred years old.

It is thought that for most of the Cretaceous period the climate of the world was relatively warm and equable, and that tropical and subtropical climates entirely suitable for the growth of forests extended from about 60 degrees north to about 60 degrees south (Barnard 1973). As late as the Eocene, the London Clay flora, at 35 degrees north, is definitely tropical (Hughes 1973). One may reasonably have some doubt about how humid the climate may have been in Nevada during the Upper Cretaceous, because of the presence of an interior drainage basin, but such Cretaceous fossil floras as we have from the western United States suggest the presence of adequate moisture.

The frequent presence of interior drainage basins in the Intermountain Region for many millions of years past tells us something about the climate. The precipitation/evaporation ratio for much of the region much of the time must have been something less than 1. At a p/e ratio of more than 1, lake basins fill and spill over, finding external drainage. It is generally considered that a p/e ratio of not less than about 1 is required to support a forest. Therefore, for much or most of its span of existence the Great Basin is not likely to have been widely forested. Other parts of the Intermountain Region appear to have had a similar climatic regimen.

ISLAND TOPOGRAPHY

The topographic diversity of the Intermountain Region, with its associated differences in temperature and moisture, effectively converts the habitats for many species of plants and animals into a series of islands. Not only the mountains, but also the valleys, form such islands for species without good means of dispersal. Birds can travel from one island to another, but small

mammals frequently cannot. Different kinds of plants likewise differ in the ability to pass the inhospitable stretches between islands.

On the other hand, these islands do not have the relative permanence of oceanic islands. The various island habitats in the Intermountain Region have expanded and merged, contracted and broken up, disappeared and reappeared, during Pleistocene and post-Pleistocene time because of changes in the climate. The principles of island biogeography, as expounded for example by MacArthur and Wilson (1967), are pertinent to the Intermountain Region, but their effect is limited by the climatically controlled changes in island area.

EARLY ANGIOSPERM EVOLUTION

The angiosperms appear to have originated early in the Cretaceous. Since we do not have fossils to connect the angiosperms to their necessarily gymnospermous ancestors, we cannot say with certainty that they did not originate somewhat earlier. The fossil record does make it clear that the evolutionary diversification of the group did not get well started until the Cretaceous. Angiosperms enter the fairly early Lower Cretaceous fossil record as an uncommon and not highly diversified group. Many of these early angiosperm fossils were at first optimistically identified with modern genera, leading to the widespread belief that the angiosperms entered the fossil record full-blown. We can now say with some assurance that the reverse is true. The pollen record speaks eloquently to the relative homogeneity of the early angiosperms, and a reexamination of the megafossils shows that their identification with modern genera was disastrously incorrect. The purportedly Jurassic palm from Utah (Tidwell et al. 1970) is clearly a palm, but it is not Jurassic. The stratigraphy of the site where it was collected is complex, and subsequent careful study shows that it is of Tertiary age (Scott et al. 1972).

The comments made in this paper on angiosperm evolution in general are heavily influenced by studies in the past decade by Dilcher (1969, 1973), Doyle (1969), Hickey (1973), Walker and Doyle (1975), Doyle and Hickey (1976), Hickey and Wolfe (1975), and Wolfe et al. (1975), who are in the forefront of the ongoing reevaluation of the early angiosperm fossil record. Their published work and my conversations with them have helped to shape my views, and I am particularly indebted to Dr. Leo Hickey for advice and counsel during the preparation of this paper. Within the Intermountain Region, the work of Axelrod (1948, 1950, 1952, 1956, 1958, 1964, 1966, 1968, 1975) is of course preeminent. Without it, our knowledge of the fossil flora would be scanty indeed. The interpretation presented is, as always, my own; those who helped me are not to be held responsible for what I might say.

The place of origin of the angiosperms is still uncertain. It is clear that they are basically a tropical group, but beyond that the situation is debatable. We can say that as early as the Aptian stage of the Lower Cretaceous, 125 million or more years ago, they were well scattered in both Gondwanaland and Laurasia, including North America, but that they did not begin to dominate the landscape until the Upper Cretaceous. There is no reason to suppose that the Intermountain Region had anything to do with the origin of the angiosperms, but at the same time it is clear enough that it has supported some angiosperms at least from the Albian stage of the lower Cretaceous to the present.

Unfortunately we can not yet see a historical connection between the Cretaceous and Tertiary angiosperm floras of the Intermountain Region, or indeed of most other parts of the world. Most of the Cretaceous genera did not persist long if at all into the Tertiary, and the limited fossil record does not show whether our early Tertiary genera originated in situ from the Cretaceous ones or migrated in from elsewhere. One of the

few Upper Cretaceous fossil floras definitely known from within the Intermountain Region is in the Blackhawk formation in central Utah, a member of the Mesa Verde Group (Parker 1968, as reported by Tidwell et al. 1972). This flora included some palms and a number of woody dicotyledons and is thought to indicate humid lowland conditions under a warm-temperate to subtropical climate. This is in general harmony with views of the Cretaceous climate of the region based on other data (e.g. Axelrod 1950).

Beginning with the Paleocene, we have a more nearly continuous history of the Intermountain flora, but even so there are some considerable gaps. Well over half of the Paleocene genera of angiosperms in the world flora are now extinct, and the fossil record as studied to date rarely shows the origin of modern genera from the more archaic ones. It appears that in the Paleocene the climate of the Intermountain Region was still reasonably warm and moist, subtropical or warm temperate, as it had been in the Upper Cretaceous.

EVOLUTION OF FLORISTIC GROUPS IN THE INTERMOUNTAIN REGION

By the middle of the Eocene, some 50 million years ago, the climate in the Intermountain Region had begun to dry out. The first indication of this in the fossil record comes in the Eocene Green River flora of northwestern Colorado and northeastern Utah (Axelrod 1950, MacGinitie 1969). This resembles the early Oligocene Florissant flora from Colorado (MacGinitie 1953) and like it may have been a subtropical savanna-woodland. No closely similar flora exists today.

Drying of the Intermountain climate continued, with some fluctuations, throughout the Tertiary. By early Oligocene the mean temperature of the world, at least in presently temperate regions, had begun to drop (Bowen 1966), and in late Oligocene it dropped markedly (Wolfe and Hopkins

1967); it never again regained the Cretaceous levels. Concomitant with increasing aridity and decreasing mean temperature in the Intermountain Region was a gradual trend toward a more continental climate, with hot, dry summers and cold, somewhat moister winters, continuing until about the middle of the Pliocene.

Floristic changes in the Intermountain Region were, of course, related to the evolutionary diversification of the angiosperms throughout the world. The monocotyledons evidently diverged from primitive dicotyledons shortly after the appearance of angiosperms in the fossil record, during the Lower Cretaceous. Palms became important elements of the world flora during the Cretaceous, and grasses in the Oligocene or earlier. Dicotyledonous herbs were rare throughout the Cretaceous and on into the Paleocene and Eocene. They began to become more abundant in the Oligocene, and they increased dramatically at the beginning of the Miocene, some 25 million years ago. During Miocene time the flora of the world began to take on a fairly modern aspect, with a great many genera that still exist today. The increase in dicotyledonous herbs in the mid-Tertiary is thought to reflect at least in part the increasing aridity of the climate throughout much of the world, enlarging the area not suitable for forests.

It is evident that during the drying of the climate in western North America the Tertiary flora sorted itself out into a more northern, mesic flora dominated by trees, and a more southern, xeric flora with few if any trees. Fossil floras from near the Oligocene-Miocene boundary in southwestern Montana suggest a mainly forest vegetation, with some elements from the drylands to the south (Becker 1969). Within the dryland flora there was a further differentiation into a more northern segment adapted to cold winters, and a more southern segment adapted to a warmer climate. The present Great Basin Floristic Province, representing the more northern of these two dryland floras, evidently took shape in the Miocene.

Indeed the Miocene boundary between the Great Basin flora and the Mohave Desert (a part of the more southern flora) may have been about where it is now (Axelrod 1950).

It is not clear how much of the differentiation of the intermountain flora during the Tertiary represents evolution in situ, and how much of it reflects immigration from other regions. Certainly both processes occurred. A similar sorting out occurred in other parts of the world, and in Eurasia this involved many of the same families and even genera. It is not likely that the same taxonomic groups originated independently in North America and Asia. There must have been some interchange.

The genus *Artemisia* might be considered in this regard. Although *Artemisia tridentata* Nutt. and its immediate allies dominate the scene in much of the Intermountain Region, *Artemisia* is not of American origin. The tribe Anthemideae of the family Asteraceae (Compositae), to which *Artemisia* belongs, is basically an Old-World tribe, and most of the species of *Artemisia* itself occur in the Old World rather than in the new. *Artemisia* and *Juniperus* characterize the landscape in parts of Armenia, for example, as well as in the Intermountain Region. *Artemisia* in the western United States is an immigrant, although the particular species we now have may well have originated here from immigrant ancestors.

Some other members of the Asteraceae are definitely American. The whole tribe Heliantheae is clearly so. Its present center of diversity is in the arid highlands of central Mexico, and it seems reasonable to suppose that the tribe is of Mexican or western American dryland origin. Many members of the group here will probably be acquainted with species of *Balsamorhiza*, *Chaenactis*, *Enceliopsis*, *Eriophyllum*, *Viguiera*, and *Wyethia*, all members of the Heliantheae, that grow in the Intermountain Region. The large genus *Haplopappus*, in the tribe Astereae, is strictly American (North and South), with one center of diversity in western North America and another in

Chile. *Erigeron* is another large genus of the Astereae that has its principal center of diversity in western North America and appears to have originated there. I am not suggesting that these several genera of Heliantheae and Astereae originated in the Intermountain Region, but they probably did not have far to come to get here.

Atriplex, another important genus in the Intermountain Region, has more species in the Old World than in the New. The family Chenopodiaceae, to which *Atriplex* belongs, has considerable concentrations of species in the Mediterranean region, in western and central Asia, in South Africa, and in Australia, as well as in the drier parts of both North and South America.

The Boraginaceae appear to be tropical and woody in origin, but they are well represented by numerous herbaceous genera and species not only in our arid West but also in the Mediterranean region and in central Asia. To what extent did our boraginaceous intermountain herbs originate in North America from tropical woody ancestors, and to what extent do they reflect immigration of herbs from the Old World? Certain genera, such as *Cryptantha* and *Plagiobothrys*, are clearly American now, whatever their eventual origin, but others, such as *Lithospermum*, are well developed in Eurasia and may well be immigrants in North America.

The Brassicaceae are well represented in the Intermountain Flora, but they are even more numerous and diversified in the arid region from central Asia to the Mediterranean, and the family as a whole is probably of Old World origin. Such familiar genera as *Lesquerella*, *Physaria*, *Stanleya*, *Strep-tanthus*, and *Thelypodium* are strictly American, whatever the origin of the family as a whole. *Cardamine*, *Lepidium*, and *Ror-ripa*, on the other hand, are well represented in the Old World also.

A few families, such as the Hydrophyllaceae and Polemoniaceae, evidently have their principal center of diversification in western North America, even if the re-

gion of their ultimate origin is not yet clearly established. Such genera as *Phacelia*, in the Hydrophyllaceae, and *Gilia*, in the Polemoniaceae (Grant 1959), are clearly at home in the Intermountain Region. There is no reason to suppose that they came in from some other continent.

Axelrod and Chaney have in various papers (e.g., Axelrod 1958) promoted the thought that the Tertiary flora of the western United States can be divided into an Arcto-Tertiary and a Madro-Tertiary segment. The Arcto-Tertiary geoflora, dominated by deciduous trees, is considered to have been very wide-spread, extending across most of northern North America and northern Eurasia. The deciduous forest of the eastern United States is considered to be the nearest modern American counterpart and a lineal descendant of the Arcto-Tertiary geoflora. The Madro-Tertiary geoflora, on the other hand, was adapted to drier, warmer conditions, with many xeromorphic shrubs, the trees being restricted to favorable habitats, or completely wanting. The Madro-Tertiary geoflora as so conceived was geographically more restricted than the Arcto-Tertiary, being confined to northern Mexico and the southwestern United States. The "Madro" part of the name comes from the Sierra Madre Occidental in northwestern Mexico. The Madro-Tertiary flora is considered to have originated in situ from subtropical western American plants that gradually became adapted (through evolution) to xeric conditions.

The concept of Arcto-Tertiary and Madro-Tertiary floras has recently been challenged by a number of authors, notably Wolfe (e.g., 1969), and is now in some disrepute. The problem, to my mind, is that some useful generalizations have been taken too literally and interpreted too rigidly. I am reminded of Gleason's challenge (1926) to Clementsian concepts of plant associations. Most modern ecologists agree with Gleason that the association is a mental construct that can be defined only arbitrarily. The idea that the community is an

organism is a good aphorism, but it can lead to serious misunderstanding if it is taken literally. Likewise the concept of an Arcto-Tertiary and a Madro-Tertiary geoflora is useful if one conceives of these floras broadly and loosely and recognizes that each of them encompasses a considerable amount of diversity, that some elements were common to both, and that there was continuous interchange between them. It is helpful to think in terms of floristic groups, but we should keep it constantly in mind that each species has its own limits of ecological tolerance, its own means of migration, and its own evolutionary potentialities, the last being influenced also by hybridization with related species. The species that make up any floristic group have entered that group, through immigration or through evolution in situ, at various times in the past, and species that are now associated may not remain associated under some future climatic regimen.

I can easily agree with Axelrod that the modern desert flora of the western United States and northern Mexico probably "developed during the Tertiary period by gradual adaptation of more mesic plants to slowly expanding dry climate" (Axelrod 1950). It seems perfectly logical to suppose that the present flora of the warm deserts south of the Intermountain Region is a lineal descendant of a Madro-Tertiary geoflora that differentiated originally from American plants adapted to similarly warm but more mesic climates. There is no other likely source. Some of them doubtless originated instead by adaptation of Arcto-Tertiary taxa to warmer, drier climates, and some of these that entered the warm deserts from the north doubtless take their origin eventually in Asia, but it strains credulity to derive the bulk of the Madro-Tertiary flora in such a way.

The origin of the Arcto-Tertiary flora is a more difficult question. Obviously it represents an adaptation of tropical or subtropical plants to a cooler but still moist climate. Since it extended across both North

America and Eurasia, one cannot a priori assume that it came principally from either an Old-World or a New World source. It seems logical to suppose that the Arcto-Tertiary flora originated from the Cretaceous tropical and subtropical Laurasian flora, but at the present time that is pure speculation. We have noted that the angiosperm fossil record as presently understood does not provide a good connection between the Cretaceous and the Tertiary. The problem is complicated by the fact that during the Mesozoic era and most of the Tertiary period North and South America appear to have been separated, not contiguous. South America was part of the southern continent, Gondwanaland, whereas North America was part of the northern continent, Laurasia. North America drifted away from Europe during and after the Cretaceous, but, until recently, it has mostly been well separated from South America. I say "mostly," because the geologic history of the Caribbean is complex and insufficiently understood, and the possibility of a direct connection between North and South America at some time during the Cretaceous or early Tertiary cannot be completely discounted.

At the present time the tropical part of the flora of North America (as represented by southern Florida, the West Indies, southern Mexico, and Central America) is clearly allied to the flora of South America. If there is any surviving Laurasian element in the present tropical North American flora, it is so thoroughly amalgamated into the Gondwanaland, South American flora that no one has yet been able to recognize it. In making this statement I exclude from consideration some primarily temperate-zone species and genera that extend into the tropics at the southern limit of their range.

Although the vegetation of most of the Intermountain Region is rather similar in aspect to that of the deserts farther south, it is very different in floristic composition. As Axelrod (1950) has pointed out, some of the dominant genera in the Intermountain Region, such as *Artemisia*, *Atriplex*, and *Cera-*

toides (*Eurotia*), apparently relate to the Arcto-Tertiary rather than the Madro-Tertiary flora. Likewise *Astragalus*, one of our largest genera in terms of number of species, has an even larger number of species in dryland Eurasia. Even if one prefers to avoid the terms Arcto-Tertiary and Madro-Tertiary, these genera still relate to Asian desert plants, presumably by way of a Beringian connection, rather than to plants from farther south in western North America. On the other hand, such large genera as *Penstemon* and *Eriogonum* are strictly American, best developed in arid western North America, without any obvious indication of a more southern (Madro-Tertiary) origin. *Haplopappus* may well be from the Madro-Tertiary, as Axelrod suggests, but its derivative *Chrysothamnus* centers in the Great Basin. We have already noted that some of the common genera of Heliantheae in the Intermountain Region may well be of Madro-Tertiary affinity. Thus it is not possible to assign the characteristic flora of the Great Basin province to either a chiefly Madro-Tertiary or a chiefly Arcto-Tertiary origin. Both of these Tertiary floras clearly contributed to the present flora of the region.

Thus, by some combination of differentiation from native elements, immigration from near and far, and proliferation of the immigrants, the Intermountain Flora acquired its special character during the Miocene epoch. Xerophytes predominated especially at lower elevations, but mesophytes survived in the moister habitats, often at higher elevations. These two types have been in continuous competition in the Intermountain Region since that time.

TENSION BETWEEN MESOPHYTIC AND XEROPHYTIC COMMUNITIES

Although the Great Basin floristic province took shape in the Miocene, it was not immediately so dry as it is now. Axelrod (1948) considers that open environments extended through the region in the Middle

Pliocene, but that the plant community was predominantly grassland, with semidesert shrubs on the drier slopes. In Miocene and Pliocene time the presently desert regions supported species comparable to those in the pinyon-juniper woodland and oak woodland that now occur at slightly higher elevations or around the borders of the desert.

Axelrod (1950) considers that the trend toward a drier, more continental climate in the Intermountain Region, begun early in the Tertiary, culminated in Middle Pliocene time, perhaps 4 or 5 million years ago. Later in the Pliocene the climate probably became a bit cooler and moister. The Pleistocene, as we all know, was marked by alternating glacial and interglacial stages. From a long-term geohistorical viewpoint, the present time may be merely another Pleistocene interglacial. Actual glaciers in the Intermountain Region were largely restricted to upper elevations in the mountains; the continental ice sheet did not reach that far south in western North America.

The glacial periods were times of relatively lower temperatures and higher p/e ratio in the Intermountain Region, cooler and more mesic than the interglacials. During the glacial periods, the mesophytes, many of them of northern floristic affinities, expanded their distribution at the expense of the xerophytes; in the interglacials the process was reversed. The great differences in elevation, together with the strong local differences in moisture relations according to slope and edaphic factors, combined with the repeated shifts in climate to keep the species populations in constant turmoil throughout the Pleistocene. T. M. Barkley (personal communication) has suggested that the blurred boundary between *Senecio streptanthifolius* (a highland species) and *Senecio multilobatus* (a lowland, more xerophytic species) in Utah reflects such hybridization. Local polyploidy helps such hybrids and hybrid segregates to persist in appropriate habitats.

Another example of the advance and re-

treat of species in the Intermountain Region due to climatic changes is provided by the oaks. In north-central Utah there exist today clones of oak that have been conclusively demonstrated to be hybrids between *Quercus gambelii* and *Q. turbinella*. *Quercus gambelii* is common in the area today, but *Q. turbinella* reaches its present northern limits more than 250 miles to the south of these hybrids. It is reasonably believed that, during the postglacial hypsithermal period, some five or six thousand years ago, the range of *Q. turbinella* extended north into north-central Utah, permitting the formation of the hybrids (Cottam et al. 1959).

Alpine fir, *Abies lasiocarpa*, provides an example in the reverse direction. According to Cottam et al. (1959), fossils discovered in 1957 by D. J. Jones demonstrate that alpine fir grew along the shores of Lake Bonneville at a time when the lake level stood well below the Provo stage. Recent fluctuations in the level of Great Salt Lake remind us that p/e ratios in the Intermountain Region continue to fluctuate, but up until now the climatic changes during the relatively short time for which we have formal, written records do not approach the magnitude of the changes that occurred during geologic time.

PRESENT-DAY CORRELATION OF ELEVATION WITH FLORISTIC GROUPS

Elevation is closely correlated with moisture relations as well as with temperature in the Intermountain Region. As one goes higher into the mountains, the temperature drops and the p/e ratio increases, and one finds a progressively more northern element in the flora. Many years ago I read somewhere that in the western United States one can roughly equate one mile of latitude with four feet of altitude. In my own experience, this conversion factor works fairly well, although there are, of course, always modifying factors to be taken into account. At moderately high elevations in the mountains, one finds many species similar or

identical to those of the northern coniferous forest, and above timberline one finds many species similar or identical to those of the modern circumboreal arctic flora. The spruce-fir forests of midupper elevations in the Intermountain Region represent a southern extension of the northern coniferous forest. Even though the dominant species are different, they compare closely with species from the northern forest. *Abies lasiocarpa* compares with *Abies balsamea*, *Picea engelmannii* and *P. pungens* compare with *P. glauca*, and *Pinus contorta* compares with *P. banksiana*. *Pseudotsuga menziesii*, on the other hand, does not have a boreal equivalent.

North of the Intermountain Region, in the northern Rocky Mountains of Canada and the northwestern United States, a very large proportion of the high-mountain species can be related directly to something from the holarctic or the northern coniferous forest. As one goes progressively southward, a larger and larger proportion of the alpine species are evidently highland derivatives from common lowland elements. In the Intermountain Region both of these types are well represented at upper altitudes. Alpine and subalpine species of *Arenaria*, *Gentiana*, *Myosotis*, *Pedicularis*, *Ranunculus*, and *Saxifraga* are likely to have boreal affinities. On the other hand, montane species of *Allium*, *Eriogonum*, *Hulsea*, *Hymenoxys*, *Lomatium*, and *Penstemon*, even at the highest elevations, generally relate to species of lower elevations, often of dry habitats. Some common montane genera, such as *Erigeron*, do not fit into either of these patterns. *Erigeron* is best developed in the western American cordillera, but the species of the dry lowlands are evidently advanced, and the more primitive species are distinctly mesophytic.

EVOLUTIONARY HISTORY OF MAMMALS

The evolutionary history of the mammals parallels in many ways that of flowering plants. Although the group takes its origin

from therapsid reptiles in the Triassic period, the placental mammals do not enter the fossil record until late in the Cretaceous. Placental mammals diversified explosively during the Paleocene, and they have been the dominant animals in terrestrial ecosystems since that time. Evolution of mammals in North America is closely correlated with that in Eurasia, but not well correlated with that in South America, because of the essential separation of North and South America until relatively recent times.

The animals that may have had the most important influence on the plants during the Tertiary period were the grazing animals—ungulates, in the broad sense. Grazing mammals began to evolve in the Paleocene or Eocene, and they reached full flower in the Oligocene and Miocene (Jones and Armstrong 1973). One may reasonably suppose that there is a relationship between the evolution of grazing mammals and the rise of grasses during the same general time. Grasses originated no later than the Oligocene, and by Miocene time they were common. The intercalary meristem of the grass leaf can reasonably be interpreted as an adaptation to grazing pressure. Thus, although it may be true that at any given time the nature of the fauna is more dependent on the flora than vice versa, in the long run the evolution of plants is strongly influenced by animals.

The most startling feature of the evolutionary history of mammals in North America was the rapid extinction of a great many of the large mammals about ten thousand years ago. There is no real parallel in the evolutionary history of plants. Similar extinction occurred to varying degrees in other parts of the world, least of all in Africa. Both climatic changes and the influence of early man have been invoked to explain the massive extinctions. In North America, the case for the predominant influence of man is very good (Martin 1967), although the subject still evokes considerable debate and difference of opinion (Axelrod 1967). The large mammals had survived much more ex-

tensive climatic changes during the Pleistocene, and their disappearance from the scene appears to be closely correlated with the spread of man. Human hunters killed the large herbivores, and many of the large predators disappeared along with their prey. Bison, camels, elephants, and horses were abundant in the Intermountain Region during the Pliocene and Pleistocene (Axelrod 1950), but of these only the bison survived the human onslaught. It is clear enough that horses, at least, are well adapted to modern conditions in the Intermountain Region, and burros do very well a little farther south. On the other hand, the camels introduced into our southwest more than a century ago did not make the grade, although they might well have done so in the absence of man.

EVOLUTIONARY HISTORY OF BIRDS

The birds apparently originated in the upper Jurassic and began to radiate in the Cretaceous, but nearly all the Cretaceous families are now extinct. After the extinction of the dinosaurs and before the evolution of large carnivorous mammals, there were some large flightless birds, which played the ecological role later taken over by large mammalian carnivores. In the northern hemisphere these birds were common from the Upper Paleocene to the middle of the Eocene. An ecologically similar but taxonomically distinct group of large, flightless, predatory birds was common from early Eocene to middle Pliocene time in South America, an area into which the large carnivores made a relatively late entry. Again the geographic separation of North America from South America during most of the time from the Cretaceous until late in the Tertiary had a profound effect on evolutionary patterns.

By the end of the Eocene the birds were highly diversified, and all living families and orders can be traced back at least that far. In Miocene time the avifauna began to take on a more modern aspect, and most of the

modern genera had come into existence by Pliocene time (Storer 1974). There was no great wave of recent extinction comparable to that of the large mammals.

The avifauna of the Intermountain Region has no endemic species and is distinguished mainly by what isn't there. The species are all more or less widespread. Distinctively Californian, southern Rocky Mountain, and Mohavean species mostly do not extend into the Intermountain Region (W. H. Behle, this symposium).

EVOLUTIONARY HISTORY OF INSECTS

The evolutionary radiation of insects, like that of flowering plants, mammals, and birds, goes back many millions of years. The Coleoptera (beetles) are well known as fossils as far back as the Permian period. The Diptera and Hymenoptera date from the Jurassic period, but only in forms such as midges and crane flies (Diptera) and saw flies (Hymenoptera), which are not and presumably never were important pollinators. The bees and the higher Diptera, which are now important pollinators, first appear in the fossil record in early Tertiary time, although they may well have originated somewhat earlier (Carpenter 1953, Baker and Hurd 1968). Most or all of the early Tertiary bees belong to extinct genera, and one may legitimately speculate that the evolution of modern bees was intimately related to the evolution of structurally complex, bee-pollinated flowers during the Tertiary. The Lepidoptera originated no later than the late Cretaceous (MacKay 1970) and had already diversified to some extent in early Tertiary time, but here again the important pollinators are apparently not ancient types. Drawing upon the recent discoveries of Cretaceous fossil insects reported by Rodendorf and Zherikhin in 1974, Doyle (1976) visualizes "major extinctions of 'Jurassic' groups within a relatively brief interval of the Late Cretaceous, and a somewhat slower rise of groups now associated with angiosperms." The coevolution of

structurally complex flowers and insects capable of recognizing complex patterns represents another example of major evolutionary interaction between plants and animals (Leppik 1957, Baker and Hurd 1968).

The faunistic differentiation between Laurasia and Gondwanaland shows up at least in the aquatic insects of the Intermountain Region. Species of Gondwanaland ancestry occur mostly in the warmer waters, or their eggs hatch relatively late in the summer. Some species of Laurasian affinity connect to Eurasia through Beringia, and others through Europe (G. F. Edmunds, personal communication).

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BIOGEOGRAPHY OF INTERMOUNTAIN FISHES

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ABSTRACT.—Eighty-three species of fishes belonging to 26 genera live in the area bounded by the Sierra Nevada, Grand Canyon, Rocky Mountains, and Snake River Plain. The waters inhabited by these fishes are part of the Great Basin, Colorado River, Snake River, upper Pit River and upper Klamath River drainages. The adaptations and distribution patterns of these fishes have been shaped by extensional faulting and volcanic activity in the Great Basin, uplift of the surrounding ranges and plateaus, and cyclic fluctuations of the Pleistocene pluvials and interpluvials. Fossil evidence indicates that in the Pliocene many of the lineages had established distributions broadly inclusive of the present-day patterns, and the subsequent trends have been extinction and some species differentiation.

Analysis of the fauna is based on designation of 48 barrier-bounded, faunally homogeneous drainage units and quantitative evaluation of patterns among species distributions and faunal similarities of drainages. Cluster analysis of species based on correlations among their patterns revealed the existence of a basic northern intermountain fluvial fauna consisting of *Cottus bairdi*, *Prosopium williamsoni*, *Catostomus platyrhynchus*, *Rhinichthys cataractae*, *Richardsonius balteatus*, and their vicariants. These fishes have similar ecology and dispersal patterns. They are ecologically associated with *Salmo clarki* (upstream) and *Rhinichthys osculus* (downstream), but these two species have broader distributions, probably because of more frequent colonization via stream capture by the former and extinction resistance by the latter. *Rhinichthys osculus* is the most widespread intermountain fish, being found in 32 of the 48 drainage units; *Gila bicolor* is next most widespread, being found in 21 units. Fifty-one of the 83 species are found in only one drainage unit; 18 of these are endemic to that unit (33 are more widespread outside the study area).

Species distributions are broader in the north, and northern and peripheral units have more species. The species:area curve for the Great Basin shows a steep slope ($z = .59$), with especially low species density in small drainages, indicating high extinction and low colonization. Postpluvial aridity, especially in the south, is the major cause of extinction and a major cause of isolation. Principal components and cluster analysis of drainage units, based on shared species, show a high correspondence between faunal similarity and geographic proximity (and weakness of barriers) and also reveal the effects of extinction in erasure of patterns. The Wasatch Range, Sierra Nevada, and southern divide boundary of the Snake River Plain have been strong barriers, leading to intensive faunal differentiation. Strong barriers and concomitant differentiation also exist in eastern Nevada, near the original center of Basin and Range tectonism. Two dozen examples of vicariant species are found to be associated with stronger-than-average barriers.

The colonization rate and extinction rate have both been accelerated in postsettlement time by introductions and habitat destruction. Most drainages and populations have been affected. Five species and many local populations have become extinct. Eighteen species and many more populations are vulnerable or threatened. Reversal of the trend will require sound ecosystem management of watersheds and restriction of exotic introductions.

The distribution patterns of fishes in the intermountain region of the western United States offer an unusual opportunity to study the evolutionary results of long-term ecological changes because of the insular nature of the drainage basins, the relatively well-known geological history, and the close dependency of these fishes on the continuity of their habitat in time and space. Their

survival has been dependent upon continuity of lakes, marshes, springs, and streams in isolated basins for many thousands of years. Dispersal has been dependent on occasional continuity of suitable habitat among basins. Compared to most kinds of organisms, the restrictions on freshwater fishes are more rigid; compared to most habitats, Great Basin aquatic habitats have been less stable

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and more confined. These restrictions provide relative constancy of some variables of interest and some replication in a quasi experiment of evolutionary responses to changing ecological conditions.

The predominant environmental factors are the degree of isolation of the drainage basins and the late Cenozoic history of fluctuating pluvial and interpluvial episodes. The isolation has greatly restricted dispersal and colonization; the fluctuating climate has subjected the fish populations to extreme conditions, forcing adaptation or extinction. Fortunately, the dominant aquatic habitats are also agents dominant in geomorphological processes, and the lakes and streams that supported the fish populations have left stark and beautiful records in their wake (Gilbert 1890, Russell 1885). This paper is a summary of the relationship of fish distributions to geological history and the contribution of fish distributional data to the understanding of that history, as reconstructed by Cope (1883), Snyder (1908, 1917), Hubbs and Miller (1948a,b), Miller and Hubbs (1960), Miller (1945, 1948, 1958, 1965), Hubbs, Miller, and Hubbs (1974) Evermann (1897), and La Rivers (1962).

GEOLOGICAL SETTING

The Great Basin includes more than 150 drainage basins among approximately 160 regularly spaced, roughly parallel mountain ranges. The ranges and valleys trend north or northeast and are bounded by steeply dipping normal faults. Faulting began as early as Eocene or Oligocene, but most of the ranges were formed during the past 20 million years by crustal extension. The Great Basin crust is relatively thin and is bounded to the east, north, and west by zones of much thicker crust. Extension has been generally northwest-southeast and has been estimated between 50 and 300 km. Geophysical evidence indicates that the driving force may be a rising, spreading, semimolten body (diapir), whose origin is related to the early and Middle Cenozoic

subduction of the Farallon plate at the West Coast trench (see Scholz et al. 1971, Atwater 1970). The structure and processes of the system are essentially those of an interarc basin. Volcanic evidence for this interpretation (from Armstrong et al. 1969) involves an episode of andesitic volcanism with much silicic ash in east-central Nevada 40-30 million years ago, abruptly changing to basaltic volcanism which radiated toward the margins of the Great Basin during the past 20 million years. Scholz et al. suggest that the outward radiation of basaltic volcanism tracked the spreading margins of the underlying diapir and its concomitant crustal extension, the whole process being initiated at the release of compressional stress when the subduction of the Farallon plate was complete.

The late Cenozoic tectonic relationship between the Great Basin and surrounding areas has been deduced from seismic data by Smith and Sbar (1974). An arcuate pattern of zones of shallow earthquakes defines the Great Basin boundary along the Snake River plain on the north, the Wasatch front on the east, and from about Cedar City west 200 km across southern Nevada on the south. Fault plane solutions indicate a slight counterclockwise rotation of the Great Basin subplate accompanied by rifting along the Snake River Plain. Volcanic activity has proceeded eastward along the Snake River Plain at a rate of about 4 cm per year, the current focus being in the Yellowstone region (Armstrong et al. 1975). This activity is interpreted by Eaton et al. (1975) and Smith and Sbar (1974) as marking the progress of a mantle plume of molten magma being overridden by the westward-moving North American plate.

This brief tectonic outline may be roughly correct, at least as far as the empirical surface history is concerned, and provides us with an indication of several of the geological variables that probably played a part in the development of patterns of distribution. It is not our intent to fit the distributions to this history, but to recognize

the antiquity of the general topographic pattern, the large potential for instability of drainage on a local scale, and the pervasive part played by volcanism.

The evolution of structural features of Great Basin and Wasatch Range topography set the stage for increasing isolation of drainage units. The degree of isolation of basins has also increased with generally increasing aridity (Axelrod 1950). During Pleistocene pluvial stages, however, considerable connectedness of drainages can be as-

sumed. Figure 1 shows maximum stands and fluvial connections of many of the larger Pleistocene lakes of the region, in addition to possible Pliocene coverage of Lake Idaho. Depicted connections and high stands were not all contemporaneous.

Little is known of early and middle Pleistocene pluvials. Older pre-Bonneville and pre-Lahontan lacustrine sediments are correlated with Cedar Ridge (Kansan) glaciation in the Rocky Mountains and are overlain by the Pearlette (restricted, type-0)

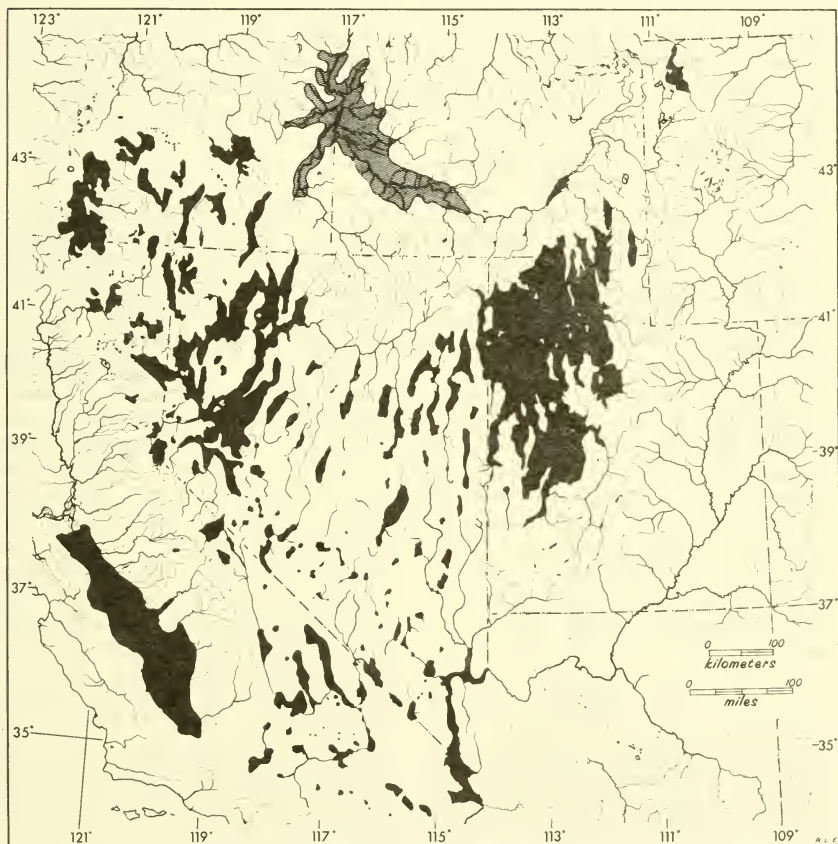


Fig. 1. Noncontemporaneous maximum extent of Late Pleistocene lakes and known fluvial connections in intermountain western North America and possible maximum extent of Pliocene Lake Idaho. Compiled and modified from Miller (1946a), Hubbs and Miller (1948), Trimball and Carr (1961), Feth (1961), Bright (193), Snyder et al. (1964), Morrison (1965), and Hubbs et al. (1974).

ash, which is 600,000 years old (Morrison 1965, Richmond 1970). Well-developed soils separate the older pre-Bonneville and pre-Lahontan sediments from younger pre-Bonneville and pre-Lahontan lacustrine sediments, believed to be contemporaneous with the Sacagawea Ridge (Illinoian) glaciation. These units are also overlain by subaerial units and soils believed correlated with the last great interglacial (Sangamon), for which dates are around 130,000 years BP (Richmond 1970).

The Alpine formation of the Bonneville Basin and Aetza formation of the Lahontan Basin are thick units of lacustrine deposits frequently interrupted by soils and subaerial zones. They appear to span a time beginning perhaps as early as 70,000 years BP, correlative with the Bull Lake glaciation. The latter portion of this period was apparently a time of intermediate lacustrine occupation of other pluvial basins as well, e.g., Searles (Smith 1968) and Yellowstone (Birkeland et al. 1971). The period from about 35,000 to 25,000 was apparently dominated by widespread subaerial deposition and soil formation (Morrison 1965, Birkeland et al. 1971).

The most recent pluvial episode, correlated with the Pinedale glaciation, has left the most abundant and clear record (e.g., probably most of the Great Basin lakes shown in Figure 1). Radiocarbon dates for high and low stages of five lakes appear to be only partly synchronous. Data for Bonneville (Morrison 1965, Bright 1966), Lahontan (Broecker and Kaufman 1965, Morrison 1965), Searles (Smith 1968), Mojave (Ore and Warren 1971), and Yellowstone (Richmond 1970) agree in showing development of generally, but not consistently, high lake levels during the period between 25,000 and 13,000 years BP. In each lake, a low stand is marked at about 11,000 years, following a high stand in the previous one or two thousand years. High levels are recorded again in the interval between 11,000 and 10,000 years, followed by low stand at about 9,000 years BP and unstable-low

stands throughout the warm period of 8,000–4,000 years BP and to the present. Lake Malheur, in the Harney Basin, shows a broadly similar pattern (Hansen 1947). Local details will be mentioned below, in connection with special distributional problems.

Although there is a tendency to look to the 13,000 and 11,000 BP lacustrine highs and their inferred associated climates for explanation of distributional patterns, it is important to remember that they represent only an unstable, late episode among a number of intermittent pluvial periods. The role of geologic and climatic factors in the manipulation of barriers and habitats will be examined by analyzing fish distributions to discover the major patterns and possible determinants of the patterns.

METHODS

Of the 70 or more major drainage basins, many are fishless and will not be considered in this study. The basins with fishes are divided into barrier-bounded, faunally homogeneous units. Criteria for barriers are presence of mountains or deserts uncrossed by continuous aquatic habitat or at least one-way restriction of fish dispersal, such as barrier falls. Criteria for homogeneity include the restriction that a drainage unit should not have two or more barrier-separated areas of endemism within it. For practical purposes, contiguous but separated small areas were often joined as one if they contained the same fauna. These criteria allowed the relatively objective designation of 48 drainage units, which are outlined and labeled in Fig. 2. To aid in ease of reference, drainage units are given initials indicating general region and faunal affinity: (B) Bonneville, (S) Snake, (O) Oregon lakes (some of which are in Nevada and California), (K) Klamath, (G) Goose (L) Lahontan, (R) Ruby group (east-central Nevada), (D) Death Valley (with Owens River and Mojave Basin), and (C) Colorado. Subsequent initials in each label refer to the specific area or some valley or ancient lake in it.

amination of the fish fossil record for data on past distributions, species density, and amounts of taxonomic change.

FISH FAUNA

The fishes inhabiting the Intermountain Region are generally classified (Bailey et al. 1970) in 83 species, 26 genera, and 7 families; 46 of the species (55 percent) and 6 of the genera (13 percent) are endemic (Table 1). In the section that follows, the species are listed with a statement of the range within and beyond the study area (abbreviations refer to drainage units in Figure 2), fossil record, and other special information. Fossil species from the region that have living representatives in the region are included in the list and marked with a +.

Petromyzontidae

Lampetra minima Bond and Kan 1973. Miller Lake Lamprey. K (Miller L., Ore.). Apparently extinct.

Lampetra tridentata (Gairdner in Richardson) 1836. Pacific lamprey. SM, K, G; coastal drainages, Alaska to S Calif., and E Asia.

Lampetra lethophaga Hubbs 1971. Pit-Klamath brook lamprey. K (upper Klamath dr., Ore.); Pit R. dr., Calif.

TABLE 1. Numbers of families, genera, and species of native fishes in the Intermountain Region, as considered in this report.

Families	Genera	Species
PETROMYZONTIDAE lampreys	1	3 (1 endemic)
ACIPENSERIDAE sturgeons	1	1
SALMONIDAE trouts, whitefish	4	10 (3 endemic)
CYPRINIDAE minnows	13 (4 endemic)	28 (14 endemic)
CATOSTOMIDAE suckers	3	21 (11 endemic)
CYPRINODONTIDAE killifishes	3 (2 endemic)	8 (8 endemic)
COTTIDAE sculpins	1	12 (6 endemic)

Acipenseridae

Acipenser transmontanus Richardson 1836. White Sturgeon. SM; coastal streams, Alaska to Calif.

Salmonidae

Salvelinus malma (Walbaum) 1792. Dolly Varden (the interior "bull trout" populations may be a distinct species [Cavender 1969]). SL (Hubbs and Miller 1948b), SM (Miller and Morton 1952), K (Bond 1973), possibly B (Rostlund 1951), but not counted in this study; freshwater and anadromous, NW N America and E Asia. Rare in Intermountain Region. Pliocene relative, west central Nevada (Cavender 1969).

Salmo clarki Richardson 1836. Cutthroat trout. BB, BP, BSV, BD, BSn, SU, SL, SW, SM, K, G, OAl, L, LE, CV, C; Western North America from headwaters of South Saskatchewan, Missouri, South Platte, Arkansas, Pecos, and Rio Grande drainages to Eel R. in N Calif. and to SE Alaska. Much local differentiation. Threatened or extinct over most of former range in Great Basin; genetically modified by introgression from cultured and introduced upper Snake River forms and *Salmo gairdneri* (Miller 1961, 1977). Pleistocene, L. Bonneville (Smith et al. 1968). Pliocene *S. esmeralda* LaRivers (1966), Esmeralda Co., Nev., may be a relative.

Salmo gairdneri Richardson 1836. Rainbow trout. SM, K; Pacific drainage, N America, from N Mexico to W Alaska, and probably headwaters of Peace and Athabaska drainage. Widely introduced.

Salmo sp. Redband trout. SM, G, OH, OAb, OSi, OW, OC; McCloud and Pit dr., Calif. (Bond 1973, LeGendre et al. 1972, LeGendre 1976).

+ *Salmo* sp. Pliocene, Lake Idaho (SM), Smith 1975, may be a relative of one or more of the above trouts.

Salmo apache Miller 1972. Arizona trout. C (upper L. Colorado dr.); Salt R. dr., Arizona. Status: threatened (Miller 1977).

Oncorhynchus tshawytscha (Walbaum)

1792. Chinook Salmon. SM; Pacific dr. from S Calif. to Hokkaido, W Arctic dr. Anadromous. Pliocene congener, *O. salax* Smith 1975, L. Idaho (SM).

Prosopium williamsoni (Girard) 1857a. Mountain whitefish. BB, BP, BSv, SU, SL, SW, SM, OH, L, C; northward in headwaters of upper Missouri, Milk, Saskatchewan, Peace, and Stikine drainages (Scott and Crossman 1973).

Prosopium abyssicola (Snyder) 1919, Bear Lake whitefish. BB (Bear L., Utah and Idaho).

Prosopium sylonotus (Snyder) 1919. Bonneville whitefish. BB (Bear L.) Pleistocene, L. Bonneville, Smith et al. 1968.

Prosopium gemniferum (Snyder) 1919. Bonneville cisco. BB (Bear L.) Pleistocene, L. Bonneville, Smith et al. 1968.

+ *Prosopium prolixus* Smith 1975, Pliocene, L. Idaho (SM).

Cyprinidae

Acrocheilus alutaceus Agassiz and Pickering 1855. Chiselmouth. SM, OH; northward in the Columbia and Fraser drainages. Pliocene relative, *A. latos* Cope, L. Idaho (SM), (Smith, 1975).

Eremichthys acros Hubbs and Miller 1948a. Desert dace. L (Soldier Meadows). Status: rare (Miller 1977).

Gila atraria (Girard) 1857b. Utah chub. BB, BT, BP, BSv, BSn, BSh, SU. Extensive local geographic variation in body size, number of gill rakers, color, etc. Pleistocene, L. Bonneville, Smith et al. 1967.

Gila coerulea (Girard) 1857b. Blue chub. K; Klamath R. Pliocene *G. milleri* Smith 1975, is a related form from L. Idaho (SM).

Gila robusta Baird and Girard 1854a. Roundtail chub. CV, CW, C. Some geographic variation.

Gila elegans Baird and Girard 1853. Bonnytail. C. Status: endangered (Miller 1977). A related form is known from the Pliocene of Arizona (Uyeno and Miller 1965).

Gila cypha Miller 1946b. Humpback chub. C. Status: endangered (Miller 1977).

Gila (Siphateles) bicolor (Girard) 1857b.

Tui chub. K, G, OH, OAb, OSm, OSi, OW, OC, OFR, OAk, L, LCl, LDm, LN, LE, LF, LDx, LT, DO, DMO, CRR. Considerable geographic variation in gill rakers, meristics, osteology, size, etc.; many well-differentiated subspecies (Snyder 1917, Miller 1973, Hubbs and Miller 1972, Hubbs et al. 1974). *Gila bicolor pectinifer* is an ecologically and morphologically divergent form that is apparently partially reproductively isolated from sympatric *G. b. bicolor* under favorable ecological circumstances in the Lahontan Basin (Hubbs et al. 1974, Hopkirk and Behnke 1966). Pliocene *Gila turneri* (Lucas 1900), (= *G. esmeralda* LaRivers 1966), Esmeralda Co., Nev., may be a relative.

Gila (Siphateles) alvordensis Hubbs and Miller 1972. Alvord chub. OAl.

Gila (Snyderichthys) copei (Jordan and Gilbert) 1880. Leatherside chub. BB, BP, BSv, SU, SW.

Hesperoleucus symmetricus (Baird and Girard) 1855. California roach. G; Sacramento dr., coastal streams, Calif.

Lotichthys phlegethontis (Cope) 1874. Least chub. BB, BP, BSv, BSn. Status: vulnerable (Miller 1977).

Richardsonius egregius (Girard) 1858. Lahontan redbreast. L, LE.

Richardsonius balteatus (Richardson) 1836. Redside shiner. BB, BT, BP, BSv, BSh, SU, SW, SM, OH; northward through the Columbia dr. to the Nass R., B. C., and the Peace R., B. C. and Alberta. The form of the Bonneville, Upper Snake, Palouse, Harney Basin (except Silvies R.) and some isolated headwaters of the M Snake, is differentiated, with fewer rays in the anal fin (*R. b. hydrophlox*). *Richardsonius durranti* of Pliocene L. Idaho (SM) is a relative (Smith 1975).

Ptychocheilus oregonensis (Richardson) 1836. Northern squawfish. SM, OH; northward through Umpqua, Siuslaw, and Columbia drainages to the Nass R., B. C., and the Peace R., B. C. and Alberta. *Ptychocheilus arciferus* of Pliocene L. Idaho (SM) is a relative (Smith 1975).

Ptychocheilus lucius Girard 1857b. Colo-

rado squawfish. *C.* Status: endangered (Miller 1977). *P. preluclus*, Pliocene of Arizona (C) is a relative (Uyeno and Miller 1965).

Mylocheilus caurinus Richardson 1836. Peamouth. SM; northward through the Columbia drainage to the Nass R. and the Peace R., B. C. *M. robustus*, Pliocene L. Idaho, is a relative (Smith 1975).

Rhinichthys cataractae (Valenciennes) 1842. Longnose dace. BB, BP, SU, SW, SM, OH; widespread throughout northern U.S. and southern Canada, north to the Mackenzie and south to N Mexico along the Rockies and from Ungava drainage south to Tennessee and North Carolina in the East.

Rhinichthys falcatus (Eigenmann and Eigenmann) 1893. Leopard dace. SM; Columbia, Fraser drainages.

Rhinichthys osculus (Girard) 1857b. Speckled dace. BB, BT, BP, BSv, BD, BSn, BSh, SU, SW, SM, K, G, OH, OAb, OSi, OW, OFR, OSp, OL, L, LCl, LE, LMd, LDm, LT, DO, DT, CV, CW, CM, CLV, C; elsewhere in Pacific drainage N. A. from the Columbia dr. of extreme southern B. C. (Scott and Crossman 1973) to northwestern Mexico (Sonora), New Mexico, Arizona and Calif. Geographically variable in meristics, color, size, and proportions (Hubbs et al. 1974).

Rhinichthys sp. BSn (Bonneville desert).

Relictus solitarius Hubbs and Miller 1972. Relict dace. RF, RSt, RW, RB.

Moapa coriacea Hubbs and Miller 1948a. Moapa dace. CW Status; endangered (Miller 1977).

Lepidomeda albivallis Miller and Hubbs 1960. White River spinedace. CW (Preston and Lund Spr., Nevada). Status: vulnerable (Miller 1977).

Lepidomeda altivelis Miller and Hubbs 1960. Pahrnagat spinedace. CW (Ash Spr. and upper Pahrnagat L., Nev.). Status: extinct.

Lepidomeda mollispinis Miller and Hubbs 1960. Virgin spinedace. CV, CM (distinct subspecies in Meadow Valley Wash, extinct). Status: vulnerable (Miller 1977).

Lepidomeda vittata Cope 1874. Little

Colorado spinedace. *C.* (Little Colorado dr.). Status: vulnerable (Miller 1977).

Plagopterus argentissimus Cope 1874. Woundfin. CV; (and formerly from the Gila R. dr.). Status: endangered (Miller 1977).

Catostomidae

Catostomus ardens Jordan and Gilbert 1880. Utah sucker. BB, BP, BSv, BD, BSn, SU. Pleistocene Lake Bonneville (Smith et al. 1968).

Catostomus macrocheilus Girard 1857b. Largescale sucker. SM, OH; northward through Columbia drainage to Nass R., B.C., and Peace R., B. C. and Alberta. (?) Pliocene and Pleistocene relatives, Lake Idaho (Smith 1975).

Catostomus occidentalis Ayres 1854. Sacramento sucker. G; Sacramento dr., and coastal drainages, Calif.

Catostomus sp. OSp (trib. Surprise Valley, Nev.).

Catostomus warnerensis Snyder 1908. Warner sucker. OW. Status: endangered (Miller 1977).

Catostomus tahoensis Gill and Jordan in Jordan 1878. Tahoe sucker. L, LE.

Catostomus fumeiventris Miller 1973. Owens sucker. DO.

Catostomus insignis Baird and Girard 1854b. Sonora sucker. CV (formerly); lower Colorado drainage.

Catostomus latipinnis Baird and Girard 1854b. Flannelmouth sucker. CV, C; lower Colorado.

Catostomus snyderi Gilbert 1898. Klamath largescale sucker. K; Klamath dr.

Catostomus catostomus (Forster) 1773. Longnose sucker. SU; northern U.S., Canada, Alaska, NE Asia.

Catostomus (Pantosteus) columbianus (Eigenmann and Eigenmann) 1893. Bridgelip sucker. SW, SM, OH; Columbia and Fraser drainages. *C. arenatus* of Pliocene Lake Idaho is a relative (Smith 1975).

Catostomus (Pantosteus) discobolus Cope 1872. Bluehead sucker. BB, SU, C.

Catostomus (Pantosteus) clarki Baird and Girard 1854b. Desert sucker. CV, CW, CM;

lower Colorado drainage.

Catostomus (Pantosteus) platyrhynchus (Cope) 1874. Mountain sucker. BB, BP, BSv, BD, BSh, SU, SM, L, C; upper Missouri, Saskatchewan, Columbia, and Fraser drainages.

Catostomus (Deltistes) luxatus Cope 1879. Lost R. sucker. K; Klamath dr., Ore., Calif. *Catostomus owyhee* of Pliocene L. Idaho is a relative (Smith 1975).

Chasmistes brevirostris Cope 1879. Short-nose sucker. K; Klamath dr. Ore., Calif. Status: vulnerable (Miller 1977).

Chasmistes cujus Cope 1883. Cui-ui. L. Status: endangered (Miller 1977).

Chasmistes liorus Jordan 1878. June sucker. BP. Status: threatened or extinct (Miller 1977).

Chasmistes sp. SU. Status: extinct. *C. spatulifer*, Pliocene L. Idaho, is a relative (Smith 1975).

+ *Chasmistes* spp. Undescribed Pliocene fossil *Chasmistes* are known from four other localities: Owens Valley dr. (DO), Madeline Plains (OMd), Fossil Lake (OFR), and the Thatcher Basin, Idaho (BB) (Miller 1965; Bright 1967).

Xyrauchen texanus (Abbott) 1861. Humpback sucker. C. Status: vulnerable (Miller 1977).

Cyprinodontidae

Empetrichthys merriami Gilbert 1893. Ash Meadows killifish. DT. Status: extinct.

Empetrichthys latos Miller 1948. Pahrump killifish. DP. Status: endangered (in refuges; extinct in native habitat) (Miller 1977). *E. erdisi* (Jordan) 1924a from the Pliocene of Ridge Basin, L.A. Co., Calif., is a relative (Uyeno and Miller 1962).

Crenichthys baileyi (Gilbert) 1893. White River springfish. CW. Status: special concern (Miller 1977).

Crenichthys nevadae Hubbs 1932. Railroad Valley springfish. CRR. Status: special concern (Miller 1977).

+ *Fundulus* spp.—Five species of Late Cenozoic *Fundulus* are known from S Calif. and Nevada (Death Valley, Mojave dr., La-

hontan dr., and Ridge Basin); they are relatives of *Empetrichthys* and *Crenichthys* (Uyeno and Miller 1962).

Cyprinodon salinus Miller 1943. Salt Creek pupfish. DMn.

Cyprinodon nevadensis Eigenmann and Eigenmann 1889. Amargosa pupfish. DMn, Dt. Geographically variable (Miller 1948, LaBounty and Deacon 1972). Status: several subspecies rare or endangered, one extinct (Miller 1977).

Cyprinodon diabolis Wales 1930. Devils Hole pupfish. DT. Status: endangered (Miller 1977).

Cyprinodon radiosus Miller 1948. Owens pupfish. DO. Status: endangered (Miller 1977).

+ *Cyprinodon brevirostris* Miller 1945, from the Tertiary of Death Valley is related to the above four species.

Cottidae

Cottus bairdi Girard 1850. Mottled sculpin. BB, BT, BP, BSv, BD, BSn, SU, SM, OH, C; Columbia drainage north to British Columbia, east through Missouri, L. Winnipeg, Hudson Bay and Ungava drainages, and across northern U.S. south to Oregon, Nevada, Utah, New Mexico, Montana, Iowa, Missouri, Alabama, and Georgia. Late Pleistocene fossil, L. Bonneville (Smith et al. 1968). Geographically variable (Bisson and Bond 1971, Bond 1963).

Cottus confusus Bailey and Bond 1963. Shorthead sculpin. SL, SM; Columbia, Puget Sound, and Flathead R. drainages.

Cottus extensus Bailey and Bond 1963. Bear L. sculpin. BB (Bear L.). Late Pleistocene fossil, L. Bonneville (Smith et al. 1968).

Cottus echinatus Bailey and Bond 1963. Utah L. sculpin. BP (Utah L.). Status: extinct.

Cottus beldingi Eigenmann and Eigenmann 1891. Piute sculpin. BB, SU, SL, SM, C (Grand R. dr., Colorado, only; not included in calculations), L; Columbia dr. Pliocene fossil, Lahontan basin (Jordan 1924, Hubbs and Miller 1948b).

Cottus leiopomus Gilbert and Evermann 1894. Wood River sculpin. SW.

Cottus greenei (Gilbert and Culver) 1898. Shoshone sculpin. SM (Thousand Springs area, mouth of Salmon Falls Cr., Idaho).

Cottus pitensis Bailey and Bond 1963. Pit sculpin. G; Pit R. dr., California and Oregon. May be extinct in Oregon (Bond 1973). *C. calcatus* Kimmel 1975 of the Miocene-Pliocene Deer Butte fm., SE Oregon, (SM), is a relative.

Cottus princeps Gilbert 1898. Klamath Lake sculpin. K (Klamath L.).

Cottus klamathensis Gilbert 1898. Marbled sculpin. K (Klamath basin); upper Pit R., Calif.

Cottus tenuis (Evermann and Meek) 1898. Slender sculpin. K (Klamath basin).

Cottus rhotheus (Smith) 1883. Torrent sculpin. SM; Columbia dr. and nearby coastal streams, Puget Sound dr., Fraser dr. southern B.C.

SIGNIFICANCE OF THE FOSSIL RECORD

Consideration of the fossil evidence, as noted among the species accounts, leads to several general conclusions that serve as a background for analysis of history of the fauna. Those conclusions are as follows.

(1) Many genera of the intermountain fish fauna were in the region, and in some of the areas presently occupied, by Pliocene time (e.g., *Prosopium*, *Salvelinus*, *Salmo*, *Oncorhynchus*, *Acrocheilus*, *Gila*, *Mylocheilus*, *Ptychocheilus*, *Richardsonius*, *Catostomus* [3 subgenera], *Chasmistes*, *Empetrichthys*, and *Cottus*).

(2) Pliocene forms are specifically different from Recent forms.

(3) Pleistocene forms are not usually specifically distinguishable from Recent counterparts.

(4) The general latitudinal gradients that exist today are also reflected in the fossil occurrences; i.e., *Cottus* was restricted to the northern regions, cyprinodontids were restricted to the southern regions, except that in pluvial periods some

northern forms (e.g., *Chasmistes*) were much further south, and in the Pliocene some faunas included forms now displaced to subarctic regions (e.g., *Myoxocephalus*) as well as forms now displaced to the south (e.g., *Orthodon*, *Mylopharodon*, *Archoplites*; Lake Idaho, Smith 1975).

(5) During some times in the past, distributions were broader and faunas larger than at present (corollary of No. 4; e.g., *Chasmistes*; Lake Idaho fauna).

ANALYSIS OF FISH DISTRIBUTIONS

What are the major patterns of distribution? From the basic data of records of native occurrence of intermountain fishes among the 48 drainage units, a matrix was computed showing the correlation of each species distribution with every other within the region. Correspondence of species patterns can be examined by similarity indices and by correlation coefficients. In this case, the product-moment correlation coefficient was found to be less sensitive to simple widespread abundance and was chosen as the basis for discussion. The correlations are summarized by a single-linkage phenogram, in which species are clustered together according to the correlation among their distributions (Fig. 3).

The general nature of the phenogram may be described in five general sections, (1) a large, rather closely clustered Klamath-Snake R.-Bonneville group; (2) a group inhabiting the Colorado Basin; (3) a small group characterizing the Lahontan Basin; (4) Owens Basin and Death Valley forms; and (5) isolated species with patterns unlike any others.

The apparent similarity of patterns of Klamath and middle Snake species is exaggerated somewhat by the fact that many of their species appear only in one or both of those units within the study area, but have diverse distributions outside. Nevertheless, the similarity of patterns among the northern drainages, including the Bonneville and

the Colorado, is much higher than among the southern drainages. Factors contributing to this phenomenon will be discussed below.

A second observation is that species of the pluvial Bonneville Basin are scattered in a number of small diverse clusters, suggesting an unusually complex history for this assemblage. Lahontan species show the same trend in a less extreme way; here, however, the scattered forms are those widespread species that are found in numerous other drainages (e.g., *Salmo clarki*, *Prosopium williamsoni*, *Rhinichthys osculus*, and *Gila bicolor*).

Relictus solitarius, which inhabits isolated basins of east central Nevada, RF, RSt, RW, and RB, has a unique distribution pattern. Of the 14 species connecting at a level more remote than .5, all but 2, *Rhinichthys osculus* and *Gila bicolor*, are restricted to very isolated, depauperate basins.

At least one cluster of species comprises widespread, ecologically similar forms, whose dispersal modes and histories might be inferred to be somewhat similar. *Cottus bairdi*, *Prosopium williamsoni*, *Richardsonius balteatus*, *Rhinichthys cataractae*, and *Catostomus platyrhynchus* are the nucleus of a Bonneville-Snake medium- and small-stream fauna; some of these, or their vicariants, are also found in the Lahontan and Colorado systems and other northern mountain drainages. They are often ecologically associated with *Salmo clarki* (upstream) and *Rhinichthys osculus* (downstream). It can also be inferred that any habitat that supports the majority of this group might well be expected to support the others. (The success of introduced *Richardsonius balteatus* in the Green River drainage is an example.) These forms, especially the trout and sculpin, occupy headwaters and as such are subject to a higher-than-average incidence of dispersal by stream capture. (A process by which "dispersal" to a new drainage system occurs without the individual fishes necessarily leaving a limited home range.) If dispersal by stream capture were the primary factor

determining the breadth of distribution of these fishes, we should see a correlation between degree of headwater habitat preference and number of drainages occupied

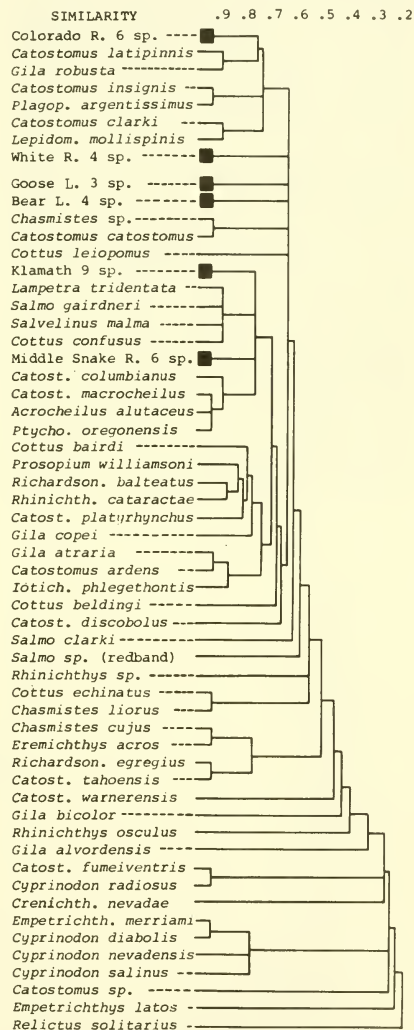


Fig. 3. Cluster analysis of 83 species of intermountain fishes based on correlation of their distributions among 48 drainage units. Species with similar patterns cluster together; species with unique or distinct patterns cluster at remote levels.

(compare species list and Figure 4). The correlation does not exist, suggesting that breadth of habitat occupiable by a species, and extinction resistance, are about as important as frequency of colonization events. The most widespread species are *Rhinichthys osculus*, 32/48 drainages, and *Gila bicolor*, 21/48 drainages. These are not particularly vagile or otherwise prone to colonization, but are interpreted to be extinction-resistant generalists with ability to persist in small streams and desert spring habitats as well as other aquatic environments. It is inferred that the distribution of these and other intermountain fishes has been shaped by a few successful colonizations and many extinctions.

The model of MacArthur and Wilson (1963, 1967) is applicable to the study of a system such as that described in the preceding paragraph. Figure 4 shows the relationship between species and the number of drainages occupied. Fifty-one of the 83 species occupy only one drainage unit in the

study area. Eighteen of these are endemic to single areas in the study; 33 are more widespread outside the area, generally in the Columbia, Pit, Klamath, or Colorado drainages. The extremely concave curve suggests a nonequilibrium situation with extinction heavily predominating over colonization.

It was noted above that longitudinal distribution of species in the north is distinctly broader than that of species in the south. This could result from any of several processes: (1) extinction may have been more severe in the south, leading to reduced ranges, (2) there may simply be more longitudinally continuous aquatic habitat in the north (omitting the Snake and Colorado drainages from the comparison) because of drainage orientations and the general northward increase in precipitation/evaporation ratios, or (3) barriers may be more extreme in the south. The fossil record, though incomplete, suggests that extinction of species has been at least as common in the north

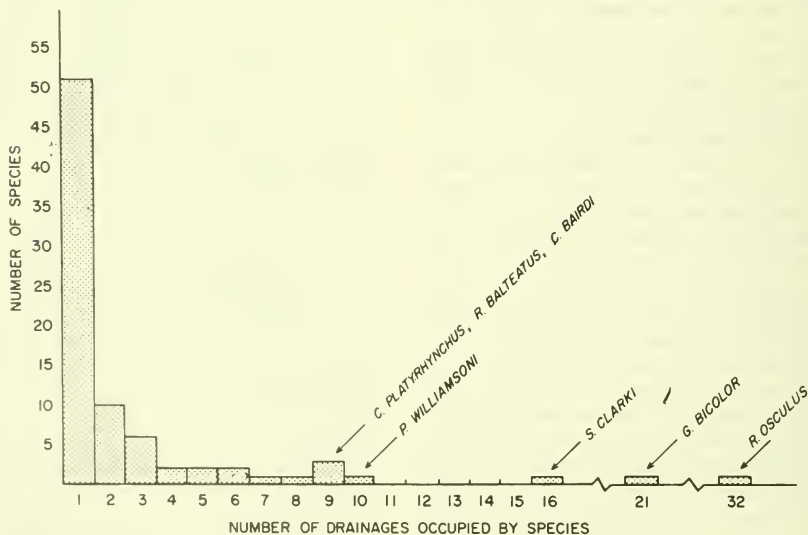


Fig. 4. Breadth of distribution of 83 species among 48 drainage units. Species are distributed according to the number of units they occupy. Fifty-one species (61 percent) are found in only one unit, 18 of these are endemic to that unit, 33 have additional range outside the study area. The steep concavity of the curve indicates much extinction and limited colonization.

and that the phenomenon exists independently of extinction, though possibly intensified by it. Factor (2) is observable and intuitively obvious as a causal agent in distribution; factor (3) involves a nonobvious principle that also may be important to the understanding of distribution patterns. Because of the well-known interaction among latitude, altitude, and temperature (e.g., Janzen 1967), the habitat of cool-stream fishes tends to be at lower altitudes in the north and higher altitudes in the south. Many northern salmonids, suckers, minnows, and sculpins show this pattern (e.g., Fig. 5). The result is that mountains of a given altitude are not as "high" in terms of barrier effects in the south, in that passes with drainage connections at 8000 ft may be occupied and accessible at 40 degrees north but not at 44 degrees north. Similarly, to these species, lowlands and valleys may be barriers in the

south, but not in the north. Conversely, to lowland, warmwater fishes such as cyprinodonts, suitable habitats "pinch out" against the hillsides at lower elevations in the north in much the same way that suitable habitats for sculpins, etc., "pinch out" at upper limits of mountain aquatic habitat in the south. That cyprinodonts and sculpins, for example, have been so ecologically and evolutionarily limited by this phenomenon in the Intermountain Region, as opposed to eastern North America, is significant (cyprinodonts range north to Canada and sculpins range south to Alabama in the east; there is almost no latitudinal overlap in the Intermountain Region).

It could be concluded that in the Intermountain Region mountain barrier effects on stream fishes decrease southward, except that an offsetting corollary also exists: the latitude-altitude-temperature effect that

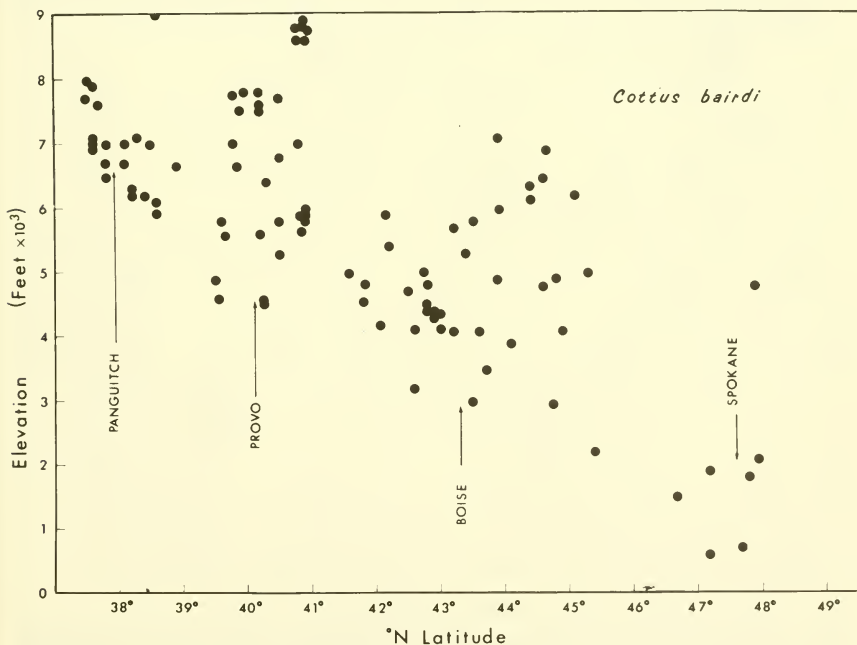


Fig. 5. Ecological gradient in habitat of 99 samples of *Cottus bairdi* from low elevations in the north to high elevations in the south.

brings temperature optima high into the mountains in the south also brings arid desert conditions and higher climatic variability to the tops of many ranges, thus providing the ultimate barrier because aquatic habitat is eliminated entirely. These are places where an observer can stand beneath dark clouds and see rain falling but not reaching the ground.

ANALYSIS OF DRAINAGE UNITS

The 48 drainage units will be compared from the standpoints of numbers of species present, similarity (shared species) of the

faunas of pairs of units, and strengths of barriers among units. The basic zoogeographic data have been accurately known since the C. L. Hubbs expeditions of the 1930s and 1940s, though different taxonomic or drainage interpretations change the numbers slightly and, in a few cases, it is not certainly known whether species are indigenous or introduced (Hubbs and Miller 1948b, Hubbs et al. 1974). It is clear from Figures 6 and 7 that northern drainages have more species, on the average. Also, large basins support more species than small basins (Fig. 8). Peripheral areas have more species on the average than those of the in-

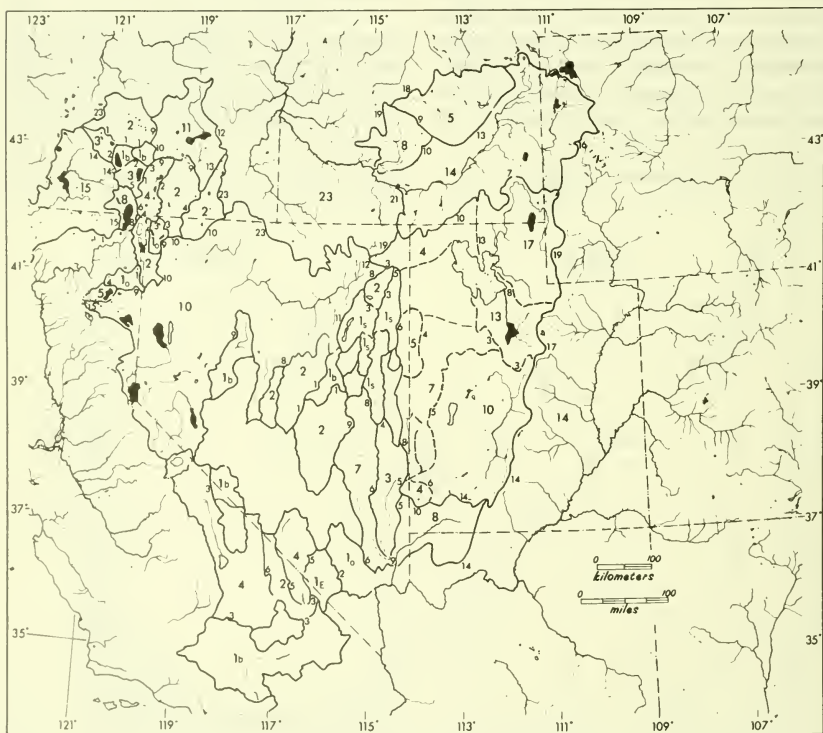


Fig. 6. Map of drainages showing major existing fluvial and lacustrine habitats, basin outlines as defined in this study, numbers of species of native fishes in each drainage unit (large, central numerals), and numbers of species of fishes limited to only one or the other side of each drainage divide barrier (small numerals near drainage divides). Breaks in dividing lines indicate probable late-pluvial connections (compare Fig. 1). See Fig. 2 for names of drainage units. Basins with no native fishes are unlabeled. Basins with single species are marked with a subscript to the numeral one indicating the inhabitant: o = *Rhinichthys osculus*, s = *Relictus solitarius*, b = *Gila bicolor*, E = *Empetrichthys latos*.

terior, probably as a result of their proximity to colonization source areas (see MacArthur and Wilson 1967), but also because areas associated with the Sierra Nevada and Wasatch mountains have higher precipitation/evaporation ratios and more aquatic habitat.

The pattern of species density among drainage areas (Figs. 4 and 7) is indicative of the degree of isolation and the frequency of extinction among Great Basin fishes. Brown (1971, 1978) showed that the distribution of boreal mammals on Great Basin mountaintop islands was characterized by fewer species, especially on small islands, than expected on the basis of the theory of extinction-colonization equilibrium. He further suggested (1971:477) that the fishes, like the mammals, colonized extensively during pluvial (and boreal flora) maxima, with subsequent isolation, reduced colonization, and increased extinction rates. A graph of log number of species of fishes against

log drainage area (Fig. 8) confirms Brown's suggestion and provides an even more extreme example. The z (slope) value for the fish example is 0.59 ($r = .66$). This value is considerably higher than the value ($z = .43$) for Great Basin mammals, indicating an extremely high extinction rate (see also Hubbs et al. 1974:79). The paucity of species in the majority of basins, especially compared with potential source areas (Figs. 6 and 7), is evidence for an extremely low colonization rate.

The strengths of the barriers among basins is shown by the small numerals next to barriers in Figure 6. The numerals give the number of species whose distribution does not cross the barrier. For example, 21 species of fishes are restricted above or below the falls of the Snake R. in units SU and SM; of the 14 species in the Colorado drainage (C) and the 13 in the Utah Lake drainage (BP), 17 species fail to cross the Wasatch Mountain barrier. (The number in

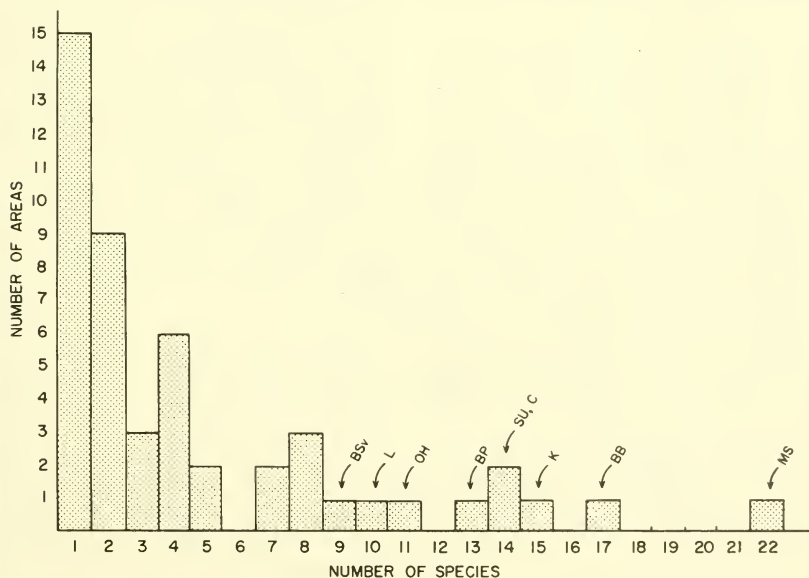


Fig. 7. Distribution of drainage units according to their species density. Of the 48 drainage units with native fishes, 24 contain only one or two species. The extreme extinction indicated by the concavity of this curve was probably intensified during the altithermal 8000–4000 years B.P. Local habitats most affected tend to single species, with sympatry relatively rare (Hubbs et al. 1974, p. 76).

common between BP and C is $((13+14) - 17)/2 = 5$).

The number of species limited by the barrier can be converted to an index showing the relative strength of the barrier, independent of species density, by dividing the number of species stopped, x , by the total number of species in the two basins. The total number, $T = (a+b+x)/2$, where a and b are the numbers of species in the two areas, and x is the number stopped at the barrier. Thus, the barrier index, $B = x/T$. The barrier index between the White River (CW) drainage and Railroad Valley (CRR) = $9/((7+2+9)/2) = 1.0$, i.e., all species stopped by the barrier. That between the northern Bonneville (BB) and the upper Snake (SU) = $7/((17+14+7)/2) = .37$.

With the exception of the last example given, for which there is a striking geological explanation in the late Wisconsin Bonneville flood (Malde 1968, Bright 1963), and the Harney Basin ($B = .52$) for which there is evidence for a stream capture (see Bisson

and Bond 1971), the index values for barriers separating the Colorado and Snake drainages C, Sm, from the Great Basin drainages are uniformly high ($B = .73-.96$). This can be taken as strong evidence for the rarity of colonization across the Wasatch divide and the southern divide of the Snake River. There is no evidence for a north-south gradient in the strength of mountain barriers. Barrier strength within the Lahontan and Bonneville basins, where differences must be largely due to differential extinction after break-up of the system, are low ($B > .6$, except where extinction has been severe but differential.) Barrier strength between the Bonneville and Lahontan Basins is high ($B = .92$), but artificially elevated by severe extinction in the north-west Bonneville Thousand Springs unit (BT). Barriers in the Mojave-Owens-Death Valley systems are strong ($B = .75-1.0$) because of the high level of taxonomic differentiation in this system (Miller 1948) and because of severe extinction.

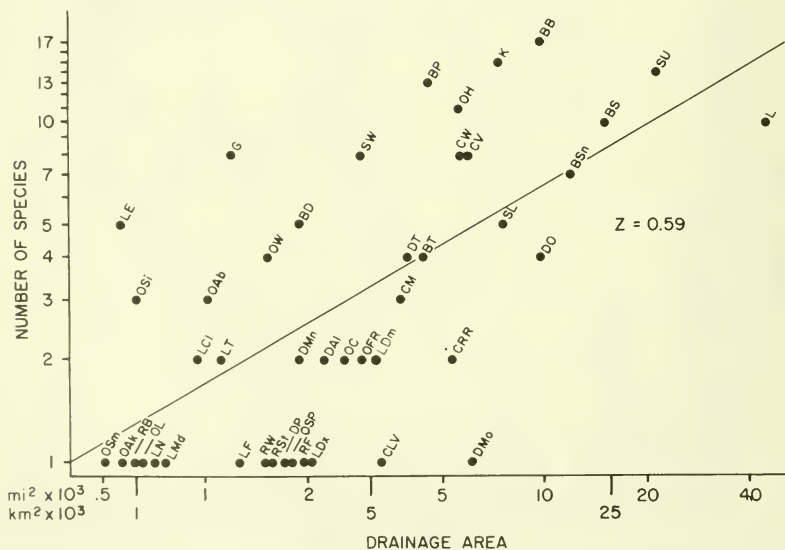


Fig. 8. The number of species in isolated Great Basin drainage units shown as a function of drainage basin area (as outlined in Fig. 1). Slope of the double logarithmic plot equals 0.59, fitted by least squares regression ($r = .66$). (Compare with similar graph in Hubbs et al. 1974:79, which shows the size of numerous fishless basins, but for which basins were defined differently and include hierarchical overlap.

In the Oregon lakes section, the values for barrier strength show the full range of possible values, probably because of different combinations of extinction. Except for the Alvord Basin, there is little evidence for isolation sufficient to produce taxonomic differentiation. The Harney Basin (OH) is a moderately isolated composite of several stages of connections to the Snake River, and at least one colonization (*Gila bicolor*) from the south (Bison and Bond 1971). The barriers between the Oregon lakes and the Klamath (K) and Goose (G) systems are relatively strong ($B = .63-.93$). Finally, the barriers associated with the central Great Basin, around the Ruby group of drainages (R-), Railroad valley (CRR), the White River system (CW), and Meadow Valley Wash (CMV) are strong ($B = .63-1.0$) and separate strongly differentiated faunas, indicating an old belt of isolation and substantial differentiation (Hubbs et al. 1974). The Virgin River system is associated with the southern part of this belt, showing a remarkable degree of isolation and differentiation from the upper Colorado drainage (14 species, $B = .78$). Part of this must be explained by recent absence of large-river fishes (*Gila elegans*, *Gila cypha*, *Ptychocheilus lucius*, *Xyrauchen texanus*) from the Virgin River, but part is the result of a center of differentiation probably dating from before the present configuration of the Colorado River in the Grand Canyon area (Hunt 1969, Metzger et al. 1973, Smith 1966).

In the above consideration of barrier effects on similarity among drainage units, no allowance has been made for phylogenetic information above the species level and its value in discovering relatively older patterns of dispersal and vicariance. The following method is developed here for adding phylogenetic information to the system. Of the various groups under consideration, only the catostomids have been studied strictly cladistically (Smith and Koehn 1969), so species groups, subgenera, and genera of other groups as currently accepted in recent

traditional taxonomic studies have been used as the source of phylogenetic information. The method is simply to add the higher taxonomic units, e.g., the *Cottus bairdi* species group (Bailey and Bond 1963), the genus *Richardsonius*, the subgenus *Pantosteus* of *Catostomus*, etc., to the taxonomic list as single taxa, recording in the data matrix each drainage unit in which they are represented. In this way, 22 higher taxa were added to the 83 species in the study—taxa which should contain evidence of older patterns of drainage connections. For example, the species in the genus *Chasmistes* individually imply no special pattern except endemism in their local areas of occurrence, but the genus *Chasmistes* as a taxon describes an ancient dispersal pattern of fundamental significance (Miller 1965) and seminal significance in zoogeographic methodology (Taylor 1960). Such data, when added to the matrix, contribute their pattern information to derived faunal indices, correlations, and summarization.

In the present study, the phylogenetically augmented data matrix was used in two ways to analyze similarity of faunal/drainage units. First, taxon-by-taxon correlation and covariance matrices were calculated (as for Fig. 3) and the principal components of these matrices were computed.

Principal component scores for drainage units were obtained by multiplication of the principal component matrices by the taxon-by-drainage data matrix. Second, Jaccard similarity coefficients were calculated to show the similarity and differences among drainage units as revealed by the shared taxa of fishes found in each. The distance (difference) matrix was summarized by a single-linkage phenogram of the drainage units.

Figure 9 combines the information of the principal component analysis and the drainage phenogram to provide a summary of faunal similarity among the drainage units. Principal axes I and II represent separate,

uncorrelated, trends among the units, and placement on the graph is according to calculated scores relative to those trends. The lines indicate levels of connection based on degree of dissimilarity (indicated by numerals) in the distance matrix. The dominant trend, representing 29 percent of the information in the data matrix, separates the rich fauna of the Snake R., Bonneville Basin, upper Colorado, Lahontan Basin, Harney Basin, and Klamath and Goose lakes, from the depauperate faunas of the more

southern basins and the small Oregon lakes units. The loadings of the taxa on principal component I indicate that the correlated distributions on which this trend is based are those of the following taxa: Salmonidae, Cottidae (especially the *bairdi* species group), *Catostomus*, *Prosopium*, *Salmo*, and their northern species. The fewer of these taxa present in a basin, the lower its score on principal component axis (P.C.) I. The strong latitudinal correlation with P.C. I results partly from dispersal, limitation, and

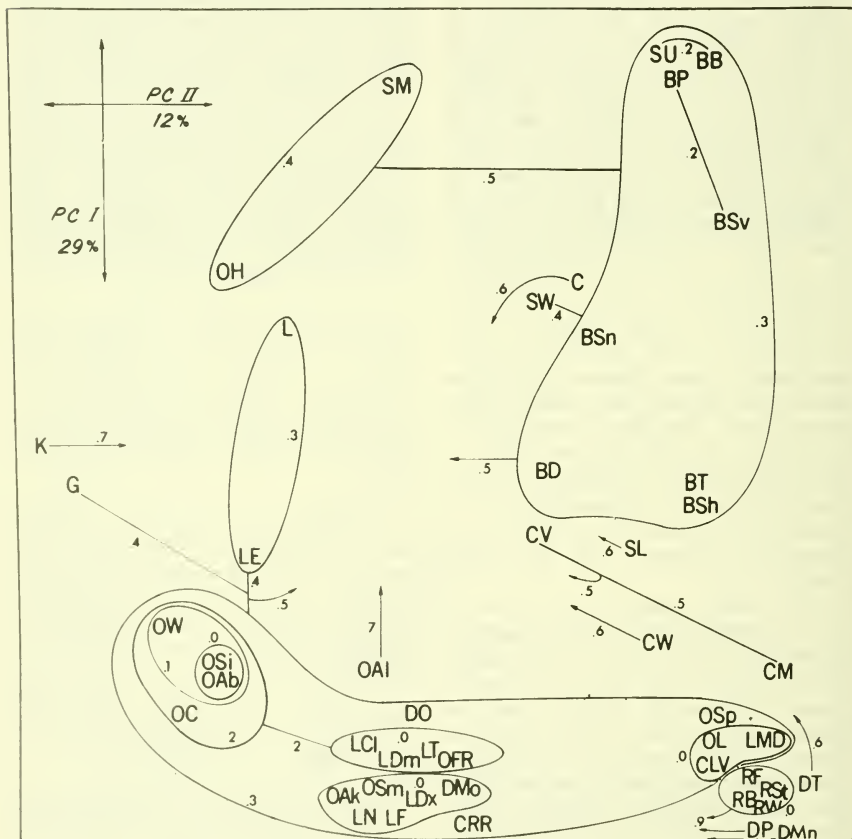


Fig. 9. Principal components (axes) and cluster analysis (lines and numerals) of patterns of fish-faunal similarity among intermountain drainage units. The letter symbols indicate the position of drainage units on the axes representing major trends in faunal similarity. The lines indicate clusters and the difference levels of branches in the clusters. Free arrows indicate separate connections to the main cluster, at the difference levels indicated by the numerals (corresponding to the outer, basal connections as in Fig. 3).

southern extinction of the basic northern Intermountain fauna.

The second trend in the principal components analysis accounts for 12 percent of the total information in the data matrix and is correlated with longitude. The Klamath, Goose, Middle Snake, Lahontan, and most Oregon lakes basins are distinguished from the Bonneville, Colorado, and associated systems. Basins with only *Rhinichthys osculus* and (or) one or two endemic species are at the extreme (lower) right of the graph. The trend is based primarily on the distribution of the subgenus *Siphateles* (*bicolor* and *alcordensis*), and to a lesser extent on the genus *Gila* (s.l.) and its relatives. The distribution of salmonids, especially the rainbow and redband trouts, are also correlated with this axis.

The cluster analysis superimposed on Figure 9 is generally corroborative of the structure of the data revealed by principal components analysis. The faunal similarities of the Bonneville group, especially its Bear River section, and the upper Snake, the Harney Basin-Middle Snake, Lahontan-Eagle Lake, and Virgin River-Meadow Valley Wash, are instructively depicted. The cluster of depauperate basins (low on P.C. I) is apparently united on the basis of general absence of most of the northern intermountain fauna. The Silver Lake-Abert Lake fauna (low on P.C. II) consists of *Rhinichthys osculus*, *Gila bicolor*, and the redband trout; the Warner drainage has, in addition, *Catostomus wamerensis*; the Catlow drainage has only *G. bicolor* and the redband trout. A cluster of six drainages (low on P.C. I; central on P.C. II) is characterized by the presence of *Gila bicolor*, only. These are the Alkali and Summer basins, Oregon; the Newark, Fish Lake, and Dixie basins, Nevada; and the Mojave drainage. Adjacent to these in the cluster analysis are four basins with *G. bicolor* and *R. osculus*: Clover Valley, Diamond Valley, and Toiyabe drainage, Nevada, and Fort Rock Basin, Oregon. Three basins have *R. osculus*, only: Long Valley, Nevada (of the

Oregon Lakes group); the Madeline Plains drainage, California; and the Las Vegas drainage, Nevada. Three unique drainages complete the large, depauperate cluster: Surprise Valley (California and Nevada) with *R. osculus* and a species of *Catostomus*; the Owens Basin, California, with *G. bicolor*, *R. osculus*, *Catostomus fumeiventris*, and *Cyprinodon radiosus*; and Railroad Valley, with *G. bicolor* and *Crenichthys nevadæ*. This large cluster is clearly based on similarity resulting from extinction, not dispersal. Data at the subspecies and racial level would be necessary for the method to discriminate and cluster in a way that would reflect fine taxonomic affinity and dispersal.

Basins with few, but distinctive, endemic species, like those of the Ruby group (Waring, Steptoe, Butte, and Franklin) and three Death Valley units (Manly, Tecopa, and Pahrump) are extreme in all aspects of the analysis, both principal components scores and level of clustering.

It is interesting that the Lahontan Basin (with Eagle Lake) joins the cluster of depauperate basins surrounding it at the 0.4 level and is immediately joined by Goose Lake. That complex joins the Bonneville-Upper Snake cluster at 0.5. The other basins then join into the Great Basin cluster at the levels indicated. The analysis clearly indicates the intimate association of the Snake R., Goose L., Colorado R., and Klamath systems to the Great Basin, notwithstanding the long isolation and evolution of endemism among these systems. The relationships and distinctive endemism of the lower Colorado group, CV, CM, and CW, are indicated by their positions and clustering level in the graph.

The trends and clusters illustrated in Figure 9 effectively summarize the faunal relationships among the drainages. The positions of drainages in the analytical space based on shared taxa is strikingly similar to their distribution in geographic space. The departure from this correspondence can be interpreted as an indication of the role of

extinction in the shaping of distribution patterns of intermountain fishes.

VICARIANCE

To what extent do the barriers separate vicariant sister species in a manner suggestive of the classical allopatric speciation model? The following examples, involving two dozen species, seem to fit the model satisfactorily. In the north, *Richardsonius balteatus* of the Bonneville-upper Snake is a sister species to *R. egregius* of the Lahontan; *Gila (Siphateles) bicolor* of the Lahontan and associated drainages is a sister species to *G. alvordensis* of the Alvord basin; *Catostomus ardens* of the Bonneville and upper Snake is a sister species to *C. macrocheilus* of the Columbia system below the falls of the Snake; *C. warnerensis* (Warner V.), *C. sp.* (Surprise V.), and *C. fumeiventris* (Owens V.) are sister species to *C. tahoensis*; *Cottus echinatus* (Utah L.) is a sister species to *C. extensus* (Bear L.).

In the south, the three species of *Lepidomeda* in the Virgin, Meadow Valley Wash, and White (Muddy) River drainages are sister species; *Crenichthys nevadae* and *C. baileyi* in the White River Valley and Railroad Valley are sister species; *Empetrichthys merriami* and *E. latos* in Tecopa Valley and Pahrump Valley are sister species; the five or six species of *Cyprinodon* in the Death Valley system are sister species; and *Catostomus (Pantosteus) discobolus* and *clarki* of the upper and lower Colorado systems are sister species. Numerous examples of more complex relationships exist (e.g. Smith 1966; Smith and Koehn 1969). The above estimates are based on cladistic inferences and phenetic similarity. Some estimates will be in error because of parallelism, convergence, or missing sister groups, just as estimates of fossil ancestors could be in error for the same reasons. The strength of 13 barriers involved in the above separations range from $B = .53$ to 1.0, with a mean of .83. Barriers not in-

volved in separation of sister species are, as expected, much lower (.23-.82, $\bar{x} = .58$) for nine barriers in the eastern Bonneville and upper Snake drainages.

Of these examples, the five species of *Cyprinodon* and two species of *Empetrichthys* in the Death Valley region (Miller 1948) and the *Cottus* from Bear Lake and Utah Lake (Smith et al. 1968) seem to represent postpluvial speciation. The time frame for the other examples is not readily known. A more detailed study of degree of differentiation and barrier chronology is required. Studies of differentiation and vicariance at subspecific levels in relation to barriers will provide detailed information about isolation effects and rates of evolution (Hubbs et al. 1974).

Several species show extensive geographic variation. *Gila bicolor* in the Lahontan, Mojave, Owens drainage, and Oregon lakes, and *Gila atraria* of the Bonneville and upper Snake are outstanding examples, showing variation in size, color, shape, osteology, gill-raker number and other meristic and morphometric characters (Hubbs and Miller 1948b, Hubbs et al. 1974, Miller 1973). The widespread *Rhinichthys osculus* varies in size, shape, colors, morphometric and meristic characters, and ecology (Hubbs et al. 1974). Other variable species are *Salmo clarki* (LeGendre et al. 1972), *Prosopium williamsoni* (Holt 1960), mountain suckers (Smith 1966), and *Cottus bairdi* (Bond 1963). The nature of the barriers and habitat gradients suggest that all species found in more than one system will show differentiation.

Sister species that are found sympatrically provide striking examples of an alternative speciation model (or possibly reinvasion after allopatric speciation). The three endemic species of *Prosopium* in Bear Lake and the sympatric ecological races of *Gila bicolor* in the Lahontan Basin (Hubbs et al. 1974) are the best examples. *Cottus* in the Klamath system and *Gila* in the Colorado drainage might be additional examples.

HISTORICAL CHANGES

In the past 100 years, extinction and colonization have greatly intensified as a result of activities of people. Five species have become extinct and 18 species are rare, vulnerable, endangered, or threatened. The most serious cause of environmental deterioration was the elimination of vegetative cover by overgrazing in the period 1880–1900, which greatly reduced the stability of rivers and other aquatic habitats (Cottam 1961, Miller 1961). There are a number of ironic examples of fish populations eliminated by flood, and many examples of streams and lakes desiccated by lack of summer flow. Diversion of surface waters and overutilization of groundwaters have depleted or eliminated many habitats. Overprotection can also be a danger: at least one population became extinct when emergent vegetation crowded out the aquatic habitat after grazers were excluded by a protective fence (J. Brown, pers. comm.).

Introduction of exotic species, mostly from the species-rich Mississippi Basin fauna, has created a situation in which most intermountain waters now have more introduced species than native species. The native species, having spent the last ten thousand or more years under extreme climatic selection, in the absence of much competition or predation, have proved ill-adapted to compete and avoid predation (Hubbs et al. 1974).

A sample of field notes and records representing collections taken over the years 1930–1960 (biased toward habitats with native populations) shows an interesting distribution (Table 2). In trout waters there are usually 0–2 native species and 1–4 introduced species. In other waters, there is a tendency for a moderate correlation between the numbers of introduced and native species. Habitat that supports a diversity of native forms tends also to support a diversity of introduced forms. Here, the colonization-extinction curve is in a new nonequilibrium: (manmade) colonizations are increasing and extinctions are accelerating almost proportionately.

DISCUSSION

The purpose of this paper is the summary and interpretation of information about distribution of intermountain fishes. Quantitative methods have been used to make the evaluation of generalized and unique patterns more objective. Some of the analyses carried out are not described in the above section, but should be mentioned for those who wish to examine the methods in more detail.

The cluster analysis of species was performed on the 83-species data set as well as the set based on 105 taxa (species and higher taxa). The latter analysis is not figured, but differs from Figure 3 in that phyloge-

TABLE 2. Summary of numbers of native and introduced species of fishes in 374 collections from the Great Basin, Upper Snake, and Upper Colorado drainages, during 1930–1960. Collections contained a mean of 2.4 native species and 0.9 introduced species.

(Column Totals)	40	108	67	55	43	49	10	2	374
	0	1	2	3	4	5	6	7	(Row Totals)
4	3	1				1	1	1	7
3	6		2	2	2	5	1		18
2	6	18	8	7	7	7	1		54
1	25	37	25	17	14	23	4		145
0		52	32	29	20	13	3	1	150

netically related forms have a slightly higher tendency to cluster near each other, partly because they tend to link through their species-group or genus if they do not have a more similar species distribution with which to cluster. Otherwise, the phenograms are identical. Without the phylogenetic information in the matrix, the results are more ecological and less evolutionary.

Principal components analyses were used because the results are readily interpretable and reveal meaningful structure. Theoretically the method is inappropriate with categorical data, but the disadvantage is insignificant, compared to the insights provided by the method. Components were calculated from the correlation and covariance matrices. The latter differ from Figure 9 in that the structure was summarized in smaller steps: the first six components accounted for 52 percent of the total information (27 percent in the first two), in ordinations that separately discriminated different drainages on the basis of the uniqueness of their faunas. The components of the correlation matrix were broader in this summarization, revealing more general trends as shown in Figure 9 (the first six components account for 66 percent of the total information).

Use of these quantitative methods is justified by the summarizations they afford and by the otherwise nonobvious insights that they provide. Examples of the latter are the discovery of the basic northern fluvial faunal unit and its relation to other species patterns (Fig. 3) and to the drainage units (discussion of Fig. 9). A second example is the factoring out and display of the extinction and dispersal effects by distortion of positions of the units in Figure 9 relative to their positions in geographic space.

The barrier analysis (Figure 6) quantified a basic (and intuitively obvious) distinction between postpluvial desiccation barriers and mountain barriers, though severe extinction in some units artificially increased the calculated barrier strength. The high barrier indices for the Wasatch Range and the

southern edge of the Snake River Plain mark zones of extreme differentiation that are also zones of tectonic interest in that they are the boundaries of the Great Basin subplate (Smith and Sbar 1974). A second zone of great barrier strength and extreme faunal differentiation is that running north-south in eastern Nevada from the Ruby Mountains to the White River drainage and Meadow Valley Wash. This zone is near the region that may mark the center from which tectonism leading to basin and range structure began and radiated outward (Armstrong et al. 1969, Scholz et al. 1971). The principal components and barrier analyses also emphasized the distinction between the faunas of the Virgin, Meadow Valley Wash, and White River drainages and that of the rest of the Colorado R., particularly that above Grand Canyon. Origin of the distinction very likely dates from the Pliocene drainage pattern associated with the interruption of the Colorado fluvial system by Hualpai Lake near the mouth of the present Colorado River Canyon in the Grand Wash Cliffs (Hunt 1956, 1969).

The problem of the Colorado River connections to the Mojave Desert is still unsolved (Hubbs and Miller 1948b) but the fact that the fauna is limited to fishes with brackish water tolerance (except for the three species from the north) suggests that the timing of the connections could date back to the Bouse embayment, some time in the Pliocene (Metzger et al. 1973:34). This suggestion is based on the assumption that a connection after recession of the embayment and the establishment of the Colorado River would have allowed colonization by lower Colorado River primary freshwater fishes as well as brackish water forms.

Finally, this analysis has proved to be a study of patterns of extinction as well as patterns of dispersal. The results indicate that the two processes are not easily separated analytically, and that studies of dispersal based strictly on cladism, ignoring extinction, are in peril of error due to missing faunas and missing sister groups.

Unfortunately the process of extinction is not restricted to the history of the present example, but is accelerating owing to land misuse and water use conflicts and is available for study as a dynamic process. Intense attention is currently focused on protection of a few individual species, but attention must soon shift to long-term maintenance of stability of aquatic habitats through management of surface waters and ground waters at the level of watershed ecosystems. Greater restraint in the introduction of exotic species would also enhance the survival of native species.

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ZOOGEOGRAPHY OF REPTILES AND AMPHIBIANS IN THE INTERMOUNTAIN REGION

Wilmer W. Tanner¹

ABSTRACT.—Few, if any, amphibians and reptiles are endemic to Utah. This is also true for much of the Great Basin, upper Colorado Plateau, southern Idaho, and Wyoming. Many species that would seemingly survive in this inland, mountainous area are not here. Only one widespread salamander and a few frogs and toads have occupied suitable habitats in the area. Lizards and snakes, like the amphibians, provide few distributions that extend throughout the area. A migration which presumably followed the Pleistocene Ice Age brought most of the species into the area as climatic conditions warmed.

Distribution maps of our modern species and subspecies indicate rather clearly that these vertebrates have invaded the Intermountain Region in relatively recent geological time. Only the periphery of Utah and adjoining states to the east and west have been penetrated by many of the species in the regional fauna.

Few, if any, of the amphibians and reptiles now present in Utah are endemic. This is perhaps also true for all intermountain states except those in the south.

There is evidence that for a period of time at the close of the Pleistocene the southern Great Basin deserts were more humid than at present. Studies of fossil pack rat middens (*Neotoma lepida*) by Wells and Jorgensen (1964), indicate that the low desert "ranges in the vicinity of Frenchman Flat (Nevada Test Site) were significantly less arid than at present. Middens now found in areas where the dominant desert shrubs are *Larrea* and *Coleogyne* have the leaves, seed, and twigs of *Juniperus osteosperma* imbedded in the crystalline urine." Wells and Jorgensen (1964) suggest that the present zonal position of the pinyon-juniper forest in southern Nevada is about 600 meters above its position of about 10,000 years ago.

The desert valleys of southern New Mexico, Arizona, and California must have been considerably more moist and humid during at least part of each year at about the same geological time as the valley floors and low foothills of southern Nevada were covered

by forests of pinyon and juniper. We assume that climatic conditions then existed which permitted considerable movement of both reptiles and amphibians.

Ballinger and Tinkle (1972) and Larsen and Tanner (1975) have assumed that there were Pleistocene refugia in the southern deserts of the United States and /or Mexico which maintained the ancestral stock from which many of the present species and subspecies of intermountain amphibian and reptilian fauna have arisen. The disjunct populations scattered throughout the "island" mountains of New Mexico and Arizona are highly suggestive of widespread populations being forced from the low valleys into cooler, moister mountains as post-Pleistocene drying slowly but continuously changed the valleys into uninhabitable deserts for many species. The xeric conditions were, however, an invitation for other species to move in, so that the lower Sonoran valleys and their associated mountain refugia now support a rich and varied series of amphibians and reptiles.

If we accept the hypothesis that there was a period of time between the cold, wet Pleistocene and the dry hot conditions of

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today when much of the southwestern United States was warm but still more humid and moist than at present, we can envision a time in which a great migration of amphibians and reptiles moved toward the plateaus and the mountainous areas of the west central United States. Nevertheless, many species of the south did not penetrate to environments in the Intermountain Region which we might expect to be compatible with their needs.

Many North American species that would seemingly survive today in intermountain environments are not here. In June 1942 I had the privilege of escorting Dr. A. H.

Wright into various habitats in central Utah. He was indeed disappointed not to find salamanders in the debris and leaf mold in and adjacent to mountain springs. Some species of Plethodontidae have reached northern Idaho and the mountains of central New Mexico. Those in Idaho are related to species along the coast from Washington south into California. We can only surmise that the ancestral stock of these species invaded our area from north central North America after the Ice Age while the northern tier of states was moist enough to permit their movement. It is puzzling why some did not persist in the Snake River Valley and the Uinta and Wasatch mountains of Utah.

At the close of the Pleistocene, some species expanded their ranges westward across the Great Plains. One example is cited by Etheridge (1961) in which fossil remains of *Ophisaurus attenuatus* were found in glacial deposits some distance west of their present range (Fig. 1a). Unfortunately, few fossils are available to substantiate the movement of other species. The disjunct ranges of many species are highly suggestive however, of the westward movement which was apparently interrupted on the high plains by rapid drying as the ice receded. A few Great Plains species did reach the mountains and are now found as isolated populations (Fig. 1b). Two genera of salamanders reached New Mexico and are found in the Jemez and Sacramento mountains of the southern part of that state: the genera are represented by *Aneides hardyi* and *Plethodon neomexicanus*. One may speculate as to why these or other genera from this large family did not reach Colorado. The best answer available is that the warming at the close of the Ice Age provided moist, warm climatic conditions in what is now the southern Great Plains but less favorable conditions on the central plains. With the ice receding from the mountains, climatic conditions in the southern Great Plains of New Mexico were apparently more moist than at present and similar to the situation

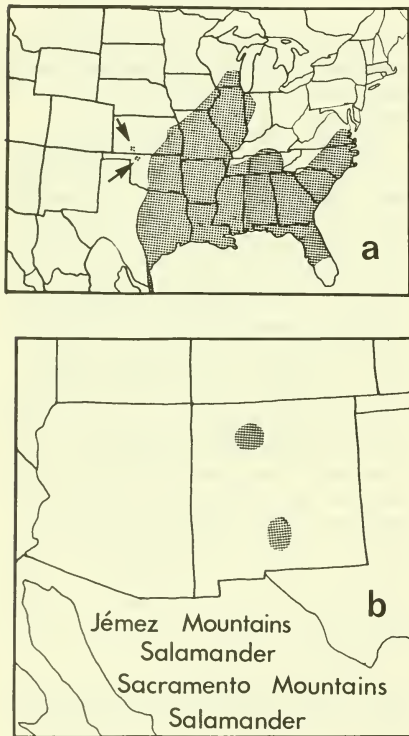


Fig. 1. (a) Known western fossil records of *Ophisaurus attenuatus*; (b) isolated populations of two plethodontid salamanders: upper, *Plethodon neomexicanus*, lower *Aneides hardyi*.

in southern Nevada about 10,000 to 15,000 years ago.

We are aware of only two plethodontid salamanders that have survived. The widespread tiger salamander may have been here during the Pleistocene. If it did exist here during the Pleistocene, it may represent one of the few species able to survive that period by remaining in the region. Once the valleys became dry, the salamanders were isolated in the mountaintops with no opportunity to expand their range. Pre-

sumably, their isolated mountain distribution and the rapidly drying conditions prevented them from reaching Colorado. To the west, north, and south of Utah the deserts developed rapidly. Glacial lakes which were present in many Great Basin valleys disappeared or were reduced to salty remnants; associated vegetation changes isolated amphibians in small areas around waterways and desert springs (Figs. 2c, 2d, and 9).

The drying out and warming of the southern portions of this vast inland area

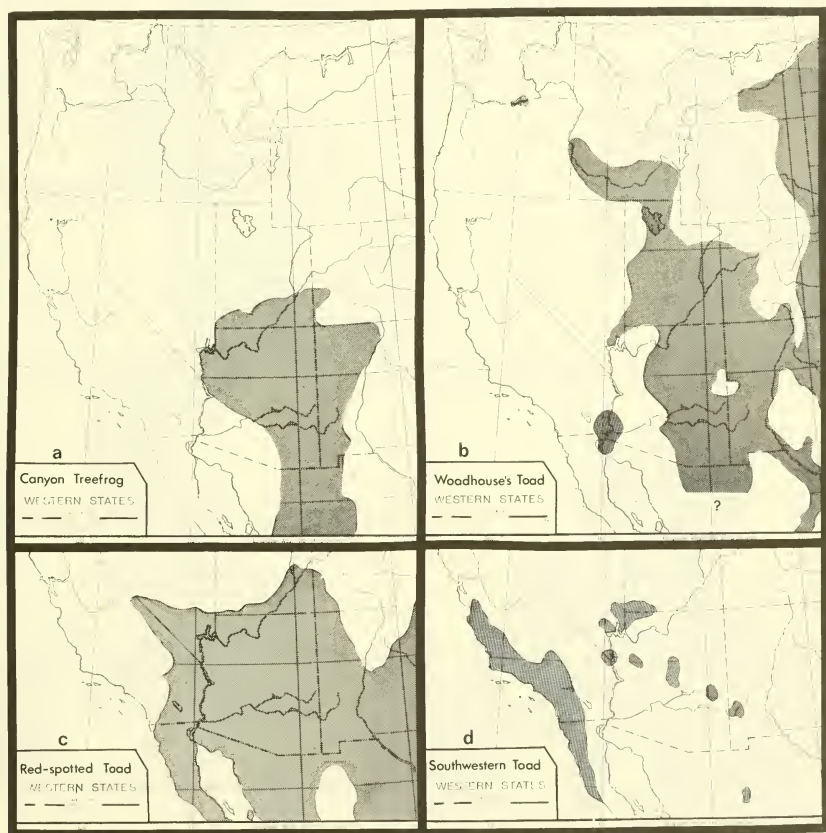


Fig. 2. Distribution of some amphibians in the southwestern United States: (a) Canyon treefrog, *Hyla arenicolor*; (b) Woodhouse's toad, *Bufo woodhousei*; (c) red-spotted toad, *Bufo punctatus*; and (d) southwestern toad, *Bufo microscaphus*.

provided an opportunity for species in the southern deserts (northern Mexico and perhaps some areas in Sonora, Chihuahua, and Coahuila) to expand their ranges northward. It is now possible to detect some such range expansions along valleys running north and west from the international border.

Time does not permit an examination of all species, but we can examine one. The leopard lizard, *Crotaphytus wislizeni*, appears to have emerged from a refugium in the Chihuahua-Coahuila area and followed routes approximately as indicated by the arrows in Figure 3a. The migration resulted

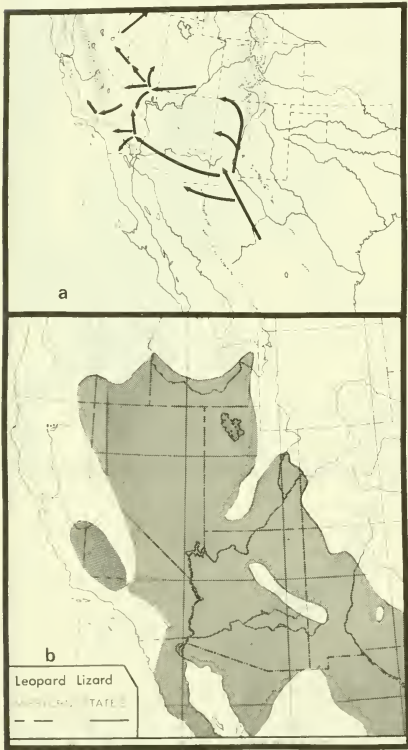


Fig. 3. (a) The theorized flow distribution for the leopard lizard *Crotaphytus wislizeni*; (b) geographical distribution as known today.

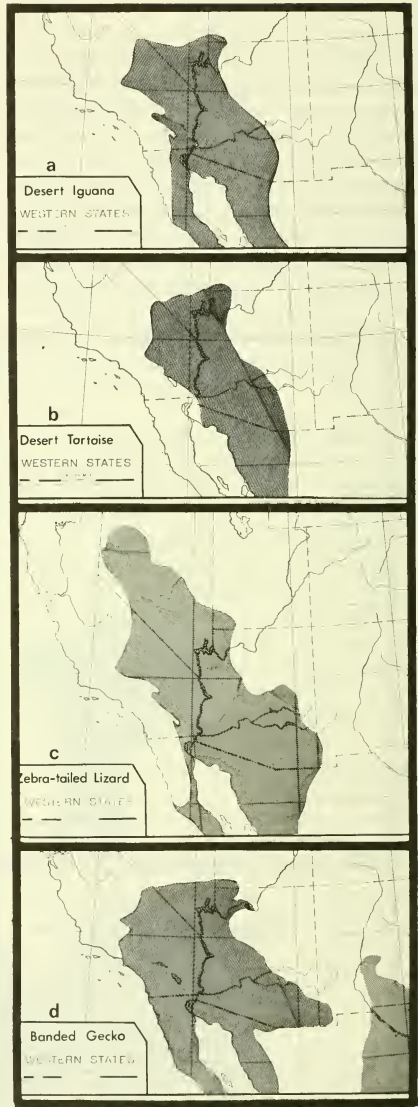


Fig. 4. Present-day distribution of southwestern reptiles: (a) desert iguana, *Dipsosaurus dorsalis*; (b) desert tortoise, *Gopherus agassizi*; (c) zebra-tailed lizard, *Callisaurus draconoides*; and (d) banded gecko, *Coleonyx variegatus*.

in the distributional pattern for the species shown in Figure 3b. In this and other species occupation of some areas produced semi-isolation, and geographical subspecies have evolved in such areas as the Colorado Plateau, Virgin River Valley, and the Great Basin of Utah and Nevada. This is true not only for the leopard lizards but for most of the species that have extended their ranges into the northern and western valleys.

Not all species moved as far or perhaps

as fast. An examination of present-day ranges are the best indicators of the general movements that occurred. The following list of 23 species (Figs. 2 and 4-8) all show range extensions into the Great Basin and the valleys of the Colorado drainage. Some species have either expanded their range more rapidly or have been able to cross elevation barriers of 5,000 feet or higher (Figs. 5 and 6) while others have not (Figs. 4 and 8).

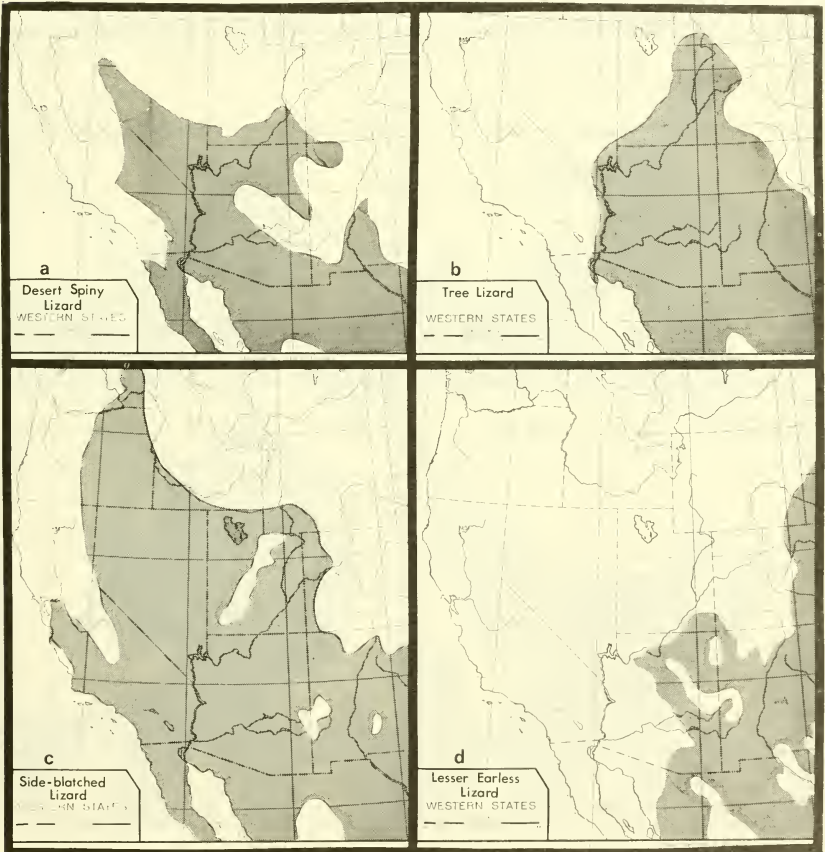


Fig. 5. Distribution of southwest reptiles: (a) Desert spiny lizard, *Sceloporus magister*; (b) tree lizard, *Urosaurus ornata*; (c) side-blotched lizard, *Uta stansburiana*; and (d) lesser earless lizard, *Holbrookia maculata*.

1. Southwestern toad (*Bufo microscaphus*)
2. Woodhouse toad (*Bufo woodhousei*)
3. Red-spotted toad (*Bufo punctatus*)
4. Canyon treefrog (*Hyla arenicolor*)
5. Desert tortoise (*Gopherus agassizi*)
6. Banded gecko (*Coleonyx variegatus*)
7. Desert iguana (*Dipsosaurus dorsalis*)
8. Zebra-tailed lizard (*Callisaurus draconoides*)
9. Lesser Earless lizard (*Holbrookia maculata*)
10. Desert spiny lizard (*Sceloporus magister*)
11. Side-blotched lizard (*Uta stansburiana*)
12. Tree lizard (*Urosaurus ornata*)
13. Western Whiptail (*Cnemidophorus tigris*)
14. Western Blind Snake (*Leptotyphlops humilis*)
15. Western Patch-nosed Snake (*Salvadora hexalepis*)
16. Coachwhip Snake (*Masticophis flagellum*)
17. Glossy Snake (*Arizona elegans*)
18. Common Kingsnake (*Lampropeltis getulus*)
19. Black-necked Garter Snake (*Thamnophis cyrtopsis*)
20. Western Ground Snake (*Sonora semianulata*)
21. Mojave Rattlesnake (*Crotalus scutulatus*)
22. Speckled Rattlesnake (*Crotalus mitchelli*)
23. Sidewinder (*Crotalus cerastes*)

Some species must have survived the Pleistocene in refugia that lay between the

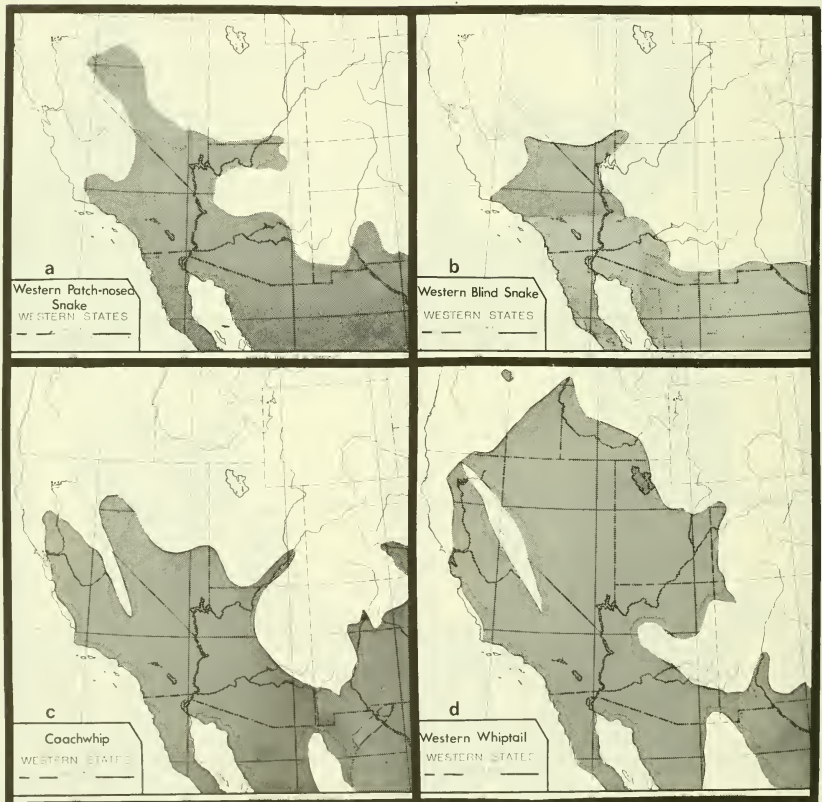


Fig. 6. Distribution of southwestern reptiles: (a) Western patchnosed snake, *Salvadora hexalepis*; (b) western blind snake, *Leptotyphlops humilis*; (c) coachwhip, *Masticophis flagellum*; and (d) western whiptail, *Cnemidophorus tigris*.

cold climates of the mountains and the drier, mild climates of southern plains. Such species include:

1. The Western Toad (*Bufo boreas*)
2. Spotted Frog (*Rana pretiosa*)
3. Rubber Boa (*Charina bottae*)
4. Western Garter Snake (*Thamnophis elegans*)

Such species seemingly have moved north as climatic conditions permitted. They occupied only mountain valleys in the southern parts of their present range (Fig. 9).

Other species have apparently moved into the Intermountain Region from the

northern or central Great Plains. Such species include:

1. The Chorus Frog (*Pseudacris triseriata*)
2. Smooth Green Snake (*Opheodrys vernalis*)
3. Racer (*Coluber constrictor*)

These are eastern species which seem to have entered through the northern Great Plains (Fig. 10). Presumably, the smooth green snake had a much wider distribution in earlier times than at present. This is indicated by its disjunct distribution.

If there are reptile species that survived the Pleistocene in the lower valleys of the Great Basin of Utah and Nevada, the short-

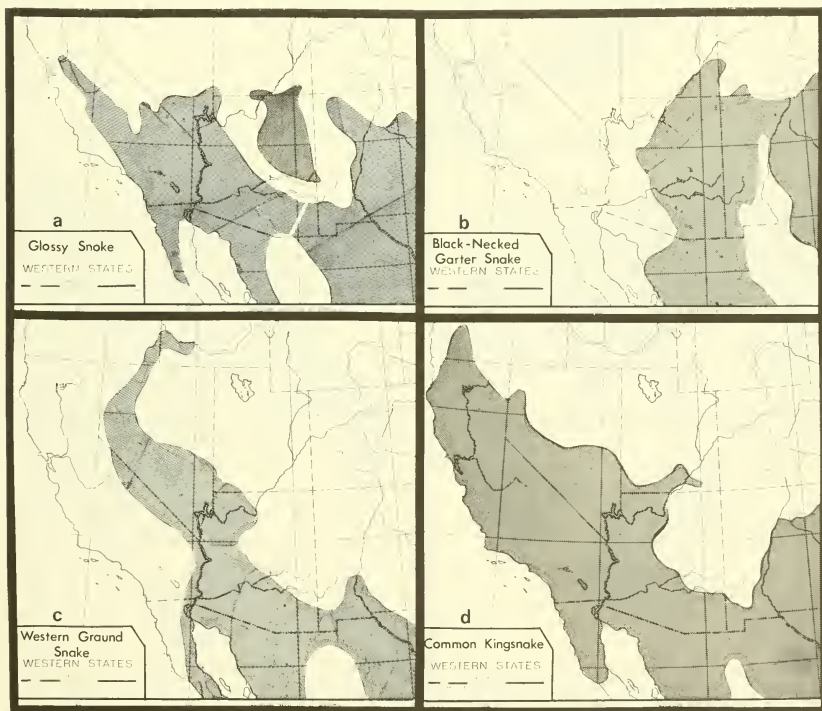


Fig. 7. Distribution of southwestern reptiles: (a) Glossy snake *Arizona elegans*; (b) black-necked garter snake, *Thamnophis cyrtopsis*; (c) western ground snake, *Sonora semianulata*; and (d) common kingsnake, *Lampropeltis getulus*.

horned lizard (*Phrynosoma douglassi*), the western skink (*Eumeces skiltonianus*), Fig. 10a), and the sagebrush lizard (*Sceloporus graciosus*) are the species most likely to have done so. These species now range from the valleys up to at least 9,000 feet in the mountains and plateaus.

In summary, we can conclude that the ancestral stocks of the great majority of present day intermountain amphibians and

reptiles originated either to the south or east of the area in question. By far the greater numbers of both amphibians and reptiles came from the south or the south-east.

The Intermountain West is a good, if not a classical, example of the David Starr Jordan theory. He stated that animals have three alternatives if radical changes occur in the environment:

1. They can follow the environment and thus remain constant.
2. They can remain and adapt to the new environment.
3. If they can do neither, they will become extinct.

It may not be possible to cite an example of a reptile or amphibian that has remained constant. Yet we do have some that have wide distributions and little morphological divergence. Two examples are the *Charina bottae* and the *Bufo boreas*. Both have wide distribution with little external variation.

Without a fossil record, we do not know how many amphibians and reptiles existed in our area since late Pleistocene time and were unsuccessful in the struggle for survival. Presumably, we have had during the last ten thousand to fifteen thousand years substantial environmental changes that offered challenges beyond the ability of some species to adapt. Other species have extended their range through adaptive radiation, which increased the number of geographical subspecies or morphological clines in the species as isolated habitats were occupied.

There is reason to believe that the movement north is still occurring. The establishment of populations of *Crotalus mitchelli* and *C. scutulatus* in Utah appear to be recent (Fig. 8). The first specimen of *C. scutulatus* was taken in 1954 and the first *C. mitchelli* in 1960. Both were taken on the southwest slope of the Beaver Dam Mountains, only a few miles inside Utah. Since then, these species have apparently expanded their ranges and are seen more often by field workers.

The northern plateau Lizard (*Sceloporus*

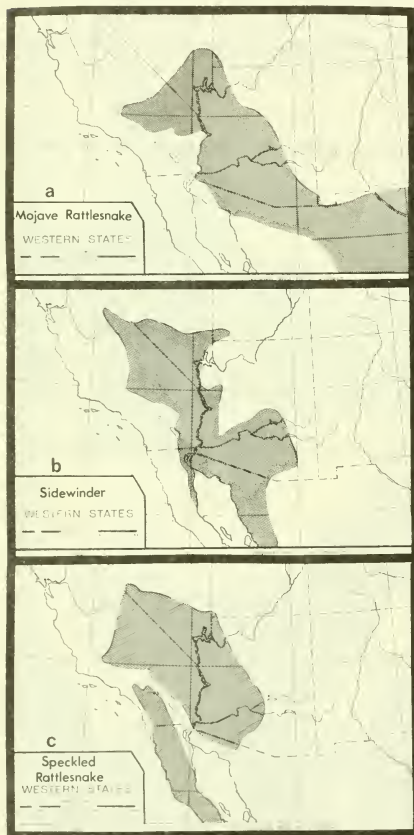


Fig. 8. Distribution of southwestern reptiles: (a) Mojave rattlesnake, *Crotalus scutulatus*; (b) sidewinder, *Crotalus cerastes*; and (c) speckled rattlesnake, *Crotalus mitchelli*.

u. elongatus) has in recent times crossed the central plateaus of Utah through the low areas between Emery and Salina and now

occurs along the foothills extending north to Ephraim and south to Monroe. We do not have records of this species west of the Se-

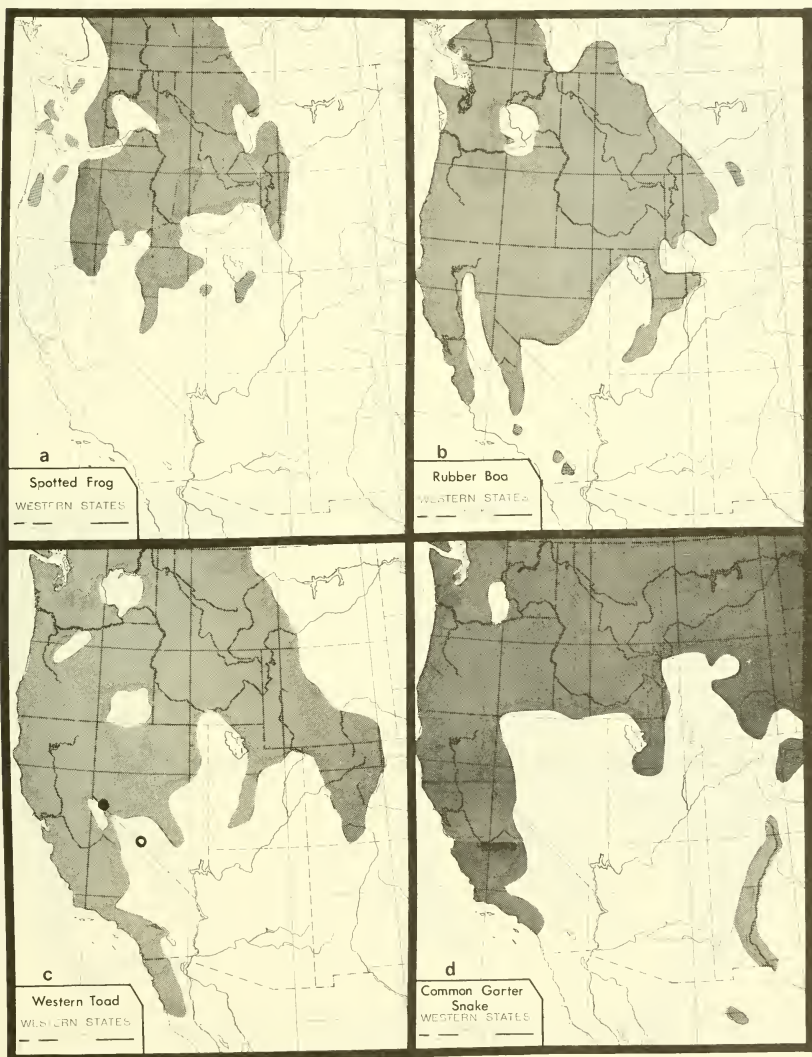
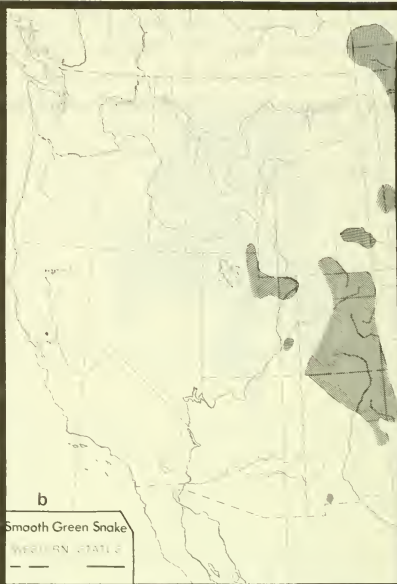


Fig. 9. Amphibians and reptiles with a more northern distribution but with populations extending south into parts of the Intermountain West and the Great Basin: (a) Spotted frog, *Rana pretiosa*; (b) rubber boa, *Charina bottae*; (c) western toad, *Bufo boreas*; and (d) common garter snake, *Thamnophis sirtalis*.



vier River. A specimen of the long-nosed snake (*Rhinocheilus lecontei*) was recently taken south of Dragerton—an indication that this species is still expanding its range.

In conclusion, it should be noted that many areas in Utah (some local, others extensive) have had their reptile populations reduced by human activity. The most common disruptive influence has been overgrazing on some private, Bureau of Land Management, and state lands.

Figures 1b, 3b, and 4-10 are taken largely from Stebbins (1966). Figure 1a is from Etheridge (1961). Even though the distribution maps have not been brought up to date for 10 years, the ranges of species used in this study have changed little.

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Fig. 10. Amphibians and reptiles which have a more northern distribution but which seemingly have entered the intermountain and Great Basin areas from the central Great Plains: a) Western skink, *Eumeces skiltonianus* [this distribution is more comparable to those in Fig. 9]; b) smooth green snake, *Ophiodrys vernalis*; c) racer, *Coluber constrictor*; and d) chorus frog, *Pseudacris nigrita*.

AVIAN BIOGEOGRAPHY OF THE GREAT BASIN AND INTERMOUNTAIN REGION

William H. Behle¹

ABSTRACT.—There are no endemic species of birds in the Great Basin. Nevertheless, a distinctive Great Basin avifauna exists which contains components of the Mojave Desert, Rocky Mountain, and Great Plains avifaunas as well as species obligate to sagebrush and the pinyon-juniper forest. Seemingly there has been little spread of California and Sierra Nevada species eastward, but a westward extension from the Rocky Mountains of several species is indicated. While several Rocky Mountain species reach their western limits on the eastern edge of the Great Basin, others have extended into the eastern portion. Two Great Plains representatives are late arrivals, namely the Baltimore Oriole and Indigo Bunting, with evidence of introgression now occurring with related western species. A similar but longstanding situation exists for the flickers. A zone of hybridization occurs in northern Utah between two species of junco. A rather abrupt junction zone between the Great Basin and Mojave Desert avifaunas exists in southern Nevada and extreme southwestern Utah. Several species representing the Mojave Desert avifauna have extended their ranges in recent years into southern Utah. Geographically variable birds show diverse patterns of distribution along with much clinal variation and intergradation. A center of differentiation for four species occurs in western Utah in the eastern portion of the Great Basin while two more occur in the western portion of the basin. The Wasatch Front is a dividing area between western and eastern races in several species. Extreme southwestern Utah constitutes a transition area where several species are represented by different races or intergradational populations. A study of the avifaunas of 14 boreal "islands" in isolated mountain ranges in western and southeastern Utah in comparison with the Rocky Mountain "continent" in central and northern Utah shows a close correlation between number of species present and habitat diversity. In addition, a low correlation exists between the number of species that are permanent residents on isolated mountains and the distance of those mountains from the "continent."

Biogeography is concerned with the distribution of organisms in time and space. Applying this to birds and the Great Basin region, it is the consensus among students of avian paleontology that most species of modern birds arose during the Pleistocene (Selander 1965), but there is virtually no fossil record of birds for the Great Basin during that interval of time. Trimble and Carr (1961) mention that bones of birds as well as of several kinds of mammals and molluscs have been found in gravel overlying the Raft Formation of American Falls Lake bed in southern Idaho which represent the late Quaternary, but no identities of the birds are given. A number of bird bones associated with prehistoric human habitations in caves in the Great Basin have been found, two of the best-known sites being Danger Cave near Wendover (Jennings

1957) and Hogup Cave near the northwestern corner of Great Salt Lake (Aikens 1970), but all the bird bones and feathers represent living species. Hall (1940) describes an ancient nesting site of White Pelicans at Rattlesnake Hill on the northeastern edge of the town of Fallon, Nevada, containing bones of White Pelicans, Double-crested Cormorants, and a Canada Goose. The bones were situated beneath a water-formed calcareous layer, which indicated that the bones had been under water at least once; but whether this was before, at, or after the time when Lake Lahonton attained its maximum level was not ascertained. The implication from the find is that the avian associates in this prehistoric time were about the same as one finds today at the colony on Anaho Island in nearby Pyramid Lake. Despite the virtual absence of a

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fossil record, it is probably safe to assume that the species of birds present in the Great Basin in the Quaternary were essentially the same as those present in the region today. With different climatic conditions, however, from time to time there have doubtless been different assemblages of birds and different distributional patterns than are seen at present. Thus, in the absence of a fossil record for the region under consideration, reliance must be placed on an analysis of the distribution of today's species in the search for clues to dispersal routes and subspecific differentiation.

Before considering the spatial dimension of the biogeography of birds of the region under consideration, it may be well to note two special items in connection with birds. One is that some birds are migratory. Thus a distinction must be made between summer residents and permanent residents. The migratory summer residents are able to easily traverse distances between mountain ranges and so are less subject to the effects of isolation than are the sedentary permanent residents. The second point is that there is a wealth of data pertaining to the distribution of birds in the collections of many museums, with much of the data readily available in published reports. For the region under consideration the following constitute the principal sources of information on the distribution of birds: for California, Grinnell and Miller (1944); for Nevada, Linsdale (1936 and 1951) and Johnson (1965, 1973, 1974); for Idaho, Burleigh (1972); for Utah, Behle (1943, 1955, 1958, 1960), Behle, Bushman and Greenhalgh (1958), Behle and Ghiselin (1958), Behle and Perry (1975), and Hayward, Cottam, Woodbury, and Frost (1976); for Colorado, Bailey and Niedrach (1965). Phillips (1958) has discussed many special problems having to do with the collecting of birds and the shortcomings of museum collections. Even though the material available falls short of the need, birds are still one of the best known groups of animals in terms of biogeography.

GREAT BASIN AVIFAUNA

Turning now to the spatial dimension, an important initial consideration is whether there is a distinctive avifauna in the Great Basin. Are the kinds of birds that occur in western Utah and Nevada different en masse from those found in the California-Sierra Nevada region on the west or the Colorado-Rocky Mountain region to the east? This query pertains only to land birds, since water birds are widespread in their occurrence throughout North America and generally show few regional distinctions except for relative abundance of particular species. An analysis of the distribution of the land birds indicates that the great majority that occur in the Great Basin range widely throughout western North America. There are about 154 kinds of resident birds in this wide-ranging category. Any distinctions, then, pertain to a relatively few kinds, but mostly it is a matter of a different combination of species in the Great Basin as compared with the assemblages in neighboring regions. Udvardy (1963: 1157) includes a Great Basin avifauna in his treatment of the bird faunas of North America, stating that the species fall geographically and ecologically into two groups, namely (1) the sagebrush-arid woodland faunal group and (2) the northwestern arid woodland faunal group. Miller (1951) in his analysis of the distribution of the birds of California includes a Great Basin avifauna as one of four faunal groups represented in the state, one that is intrusive into northeastern California east of the Sierran crest. He states that the Great Basin avifauna consists of two categories: (1) species of interior continental derivation that occur south of or below the boreal areas, and (2) geographic races that have differentiated in the Great Basin at austral levels. He designates 35 kinds as belonging to the Great Basin avifauna. Johnson (1975) followed Miller in his treatment of a Great Basin avifauna.

Probably the most distinctive feature about the Great Basin avifauna is the pres-

ence of certain birds that are associated with two plant formations that occur widely throughout the region, namely big sage (*Artemisia tridentata*) and the pinyon-juniper woodland. Birds that occur almost exclusively in stands of sagebrush are the Sage Grouse, Sage Thrasher, and Sage Sparrow. Birds that occur chiefly, if not exclusively, in the pygmy woodland, which itself has much sage interspersed with the junipers and pinyon pines, are the Cassin's Kingbird, Gray Flycatcher, Scrub Jay, Pinyon Jay, Plain Titmouse, Bush-tit, Blue-Gray Gnatcatcher, Cedar Waxwing, Gray Vireo, Black-throated Gray Warbler, and Brewer's Sparrow. However, the pygmy woodland occurs throughout the Southwest so these associated species of birds occur in areas beyond the Great Basin. To properly characterize the Great Basin avifauna, comparisons with surrounding regions are necessary.

There are about 30 kinds of distinctive birds that occur in the California-Pacific Coast-Sierra Nevada region that are not known to occur in either the Great Basin or the Rocky Mountains. Many are endemic to the West Coast area and constitute the most conspicuous elements of the California avifauna. Some of these, such as the Mountain Quail and White-headed Woodpecker, occur in the Sierra Nevada on the western rim of the Great Basin, but I find little evidence of these distinctive California forms spilling over eastward into the mountain ranges in the Great Basin. Several northern birds reach the southern limits of their ranges, at least in part in the Great Basin. These are the Marsh Hawk, Roughleg Grouse, Sharp-tailed Grouse, Sage Grouse, Lewis Woodpecker, Tree Swallow, Swainson's Thrush, Water Pipit, American Redstart, and Fox Sparrow. Many southern birds reach their northern limits, in at least part of their range, in the Great Basin. These are the Whip-poor-will, Black Phoebe, Gray Flycatcher, Plain Titmouse, Bewick's Wren, Bendire's Thrasher, Blue-gray Gnatcatcher, Gray Vireo, Virginia's

Warbler, Black-throated Gray Warbler, Painted Redstart, Scott's Oriole, Lesser Goldfinch, Black-throated Sparrow, Gray-headed Junco, and Black-chinned Sparrow. There are about 25 kinds representing the Mojave Desert avifauna that occur in southeastern Nevada and southwestern Utah but which do not penetrate any farther north into the Great Basin except on an accidental basis. These are discussed in the following section of this paper.

Nineteen kinds of birds occur in Colorado that do not occur as breeders in either the Great Basin or California areas. Mostly these are species of the Great Plains avifauna that reach the western limits of their ranges along the east base of the Rocky Mountains. One species is endemic to the mountains of Colorado, namely the Gray-crowned Rosy Finch. There are several species that occur as breeders in both the Rocky Mountains and the Great Basin which do not occur in the California-Sierra Nevada area. Thus they reach their western limits within the Great Basin. These are the Northern Three-toed Woodpecker, Catbird, Brown Thrasher, Veery, Water Pipit, Black Rosy Finch and Indigo Bunting. None of these are common in the Great Basin and at least two, the Brown Thrasher and Indigo Bunting, appear to be late arrivals in the region west of the Rocky Mountains. Three species are found at the eastern edge of the Great Basin in Utah but are not known to occur in the basin per se. These are the Purple Martin, Gray Jay, and Pine Grosbeak. Several kinds are essentially restricted in Utah in their breeding range to the Colorado River drainage system, but occasionally individuals occur in the Great Basin as accidents. These are the Gambel Quail, Costa Hummingbird, Roadrunner, Bendire's Thrasher, and Blue Grosbeak. Finally, I know of no species of bird that is endemic to the Great Basin.

From all this we can conclude that there is a distinctive Great Basin avifauna but it is one that is not characterized by endemic species. Rather it is recognizable on the

basis of a different assemblage of birds, many of which are intrusive from surrounding regions. There is more evidence of a western spread of eastern species into the Great Basin than there is of an eastward spread from the Sierra Nevada-California area. Because of the lack of endemics, the Great Basin avifauna is not as distinctive as surrounding avifaunas, but it is more sharply confined, being delimited on the west by the Cascade-Sierra cordillera and on the east by such outlying ranges of the Rockies as the Wasatch Mountains of northern Utah and the high plateaus of central Utah. On the south the Great Basin avifauna meets the Mojave Desert avifauna in a rather distinct and narrow junction zone. There is no comparable junction zone or mountain barrier at the northern limits of the Great Basin. Here the Great Basin species gradually merge with those of either the western woodland edge or those of the open Palouse country east of the Cascades.

RELATIONS OF MOJAVE DESERT AND
GREAT BASIN AVIFAUNAS IN SOUTHWESTERN
UTAH
AND SOUTHEASTERN NEVADA

The northern limits of the Mojave Desert Biome in Nevada have been mapped by Gullion et al. (1959: 279). Areas included are Meadow Valley Wash, Muddy River, and Pahrangat Valley. In southwestern Utah, the warm southern desert occurs along the floor of the Virgin River Valley to the mouth of Zion Canyon near Springdale (including Coal Pits Wash) as well as along the lower stretches of tributary streams such as La Verkin, Ash, and Santa Clara creeks and Beaver Dam Wash on the west side of the Beaver Dam Mountains. In Arizona it occurs along the Virgin River Valley. There are 28 kinds of summer resident birds in this region that are representatives of the Mojave Desert avifauna. Fifteen of these are known to occur in Utah only in this area. The other 13 occur there regularly but a few extralimital records exist

elsewhere in the state. The Mojave Desert avian indicators are the Black Hawk, Gambel's Quail, White-winged Dove, Ground Dove, Inca Dove, Roadrunner, Lesser Nighthawk, Costa's Hummingbird, Rivoli's Hummingbird, Ladderbacked Woodpecker, Wied's Crested Flycatcher, Black Phoebe, Vermilion Flycatcher, Verdin, Cactus Wren, Le Conte's Thrasher, Crissal Thrasher, Black-tailed Gnatcatcher, Phainopepla, Bell's Vireo, Lucy's Warbler, Painted Redstart, Hooded Oriole, Scott's Oriole, Summer Tanager, Blue Grosbeak, Abert's Towhee, and Rufous-crowned Sparrow. Several of these species seem to have extended their ranges into southwestern Utah in recent years, namely, the Black Hawk, White-winged Dove, Inca Dove, Rivoli's Hummingbird, Wied's Crested Flycatcher, Black-tailed Gnatcatcher, Summer Tanager, and possibly the Rufous-crowned Sparrow, although the latter may represent an overlooked species associated with a relict grassland habitat. A summary of records and details of distribution for this complement of birds has recently been presented by Behle (1976b) for the three-state region. Immediately to the north of this Mojave Desert or Lower Sonoran area and at higher elevations in the region in the pinyon-juniper belt, birds are found that represent the Great Basin avifauna.

There are some aspects of subspecies distribution and intergradation in extreme southwestern Utah that are significant in terms of southern derivations of the population. These are discussed elsewhere in this paper. The hybridization that produces intergradation in these several species, as well as increased variability in the populations, suggests the presence of a suture zone, using the terminology of Remington (1968). He defined a suture zone as "a band, whether narrow or broad, of geographic overlap between major biotic assemblages, including some pairs of species or semi-species which hybridize in the zone." As Uzzell and Ashmole (1970) further note, suture zones stand to biotas as zones of sec-

ondary intergradation stand to pairs of populations. Unless one prefers to regard the Gilded Flicker as a separate species from the Red-shafted Flicker, to my knowledge no hybridization occurs in extreme southwestern Utah at the species level. Rather, the crossing is between representatives of different subspecies producing intermediate and highly variable populations where, in addition to the intergrades, typical representatives of the two parental stocks occur. In the region to the north of the Virgin River Valley, some cases are known where introgression has taken place. These are discussed in another section of this paper.

BOREAL ISLANDS AND EFFECTS OF ISOLATION

One of the most significant aspects of zoogeography in the Great Basin and Intermountain Region pertains to the discontinuous occurrence of boreal species on the many isolated mountaintops of the region. The distribution of birds on 31 such islands has been discussed by Johnson (1975) in a study patterned after similar studies by Brown (1971) on mammals of the Great Basin ranges and Vuilleumier (1970) on birds in the páramo islands in the northern Andes. Although Johnson had data available from several of my reports for certain islands in western Utah which constituted the eastern fringe of his study area, additional data for Utah have been mobilized for this paper to extend Johnson's study. Although I have followed his procedures, our data are not precisely comparable because of regional differences in the avifauna, my elimination of water birds from the boreal category, and the circumstance that I have followed Brown's approach of considering as boreal species those that occur above 7500 feet elevation rather than attempting to determine the lower edge of the forest woodland. The 80 species that I have designated as boreal are listed in the Appendix along with an indication of their presence or absence on the 14 boreal islands studied in western and southeastern Utah. The basic

data for the several islands are presented in Table 1. These data were first subjected to a normality check which showed that they fit a normal distribution in an untransformed condition. The data were then analyzed by means of a partial correlation analysis which showed that three variables, namely elevation of highest peak, total area, and habitat diversity score (HDS) were highly correlated. Then a stepwise multiple regression study showed that HDS had the highest correlation with the total number of bird species occurring. The R-value (correlation coefficient) was .86, which was significant at the .001 level. Because of the intercorrelation among the three independent variables, the multiple regression analysis was run first with HDS included in the equation while excluding elevation and total area. Then it was run excluding HDS but including elevation and area. Finally calculations were made including all three variables. As is indicated by the data summarized in Table 3 and the adjusted R^2 values, the effect of multicollinearity is present when all three variables are included in the equation. Although not as strong, these results follow those of Johnson closely. Because of the multicollinearity when all three independent variables were included in the equation, the R^2 value given in Figure 2 (which is .75) is the value derived from the equation excluding elevation and total area. The results shown in Figure 2 are similar to those of Johnson (1975: 553).

Although there is a high correlation between the number of kinds of birds occurring and general habitat diversity as represented by the habitat diversity scores, there is the complication that the HDS involves many environmental variables. In attempting to identify particular aspects of the habitat community structure that control the kinds and number of species present, Johnson (1975: 555) analyzed the species composition of the boreal birds and their ecologic rolls in the community. He divided them into two groups: "Restricted," which occurred in 5 or fewer of his 31 sample areas,

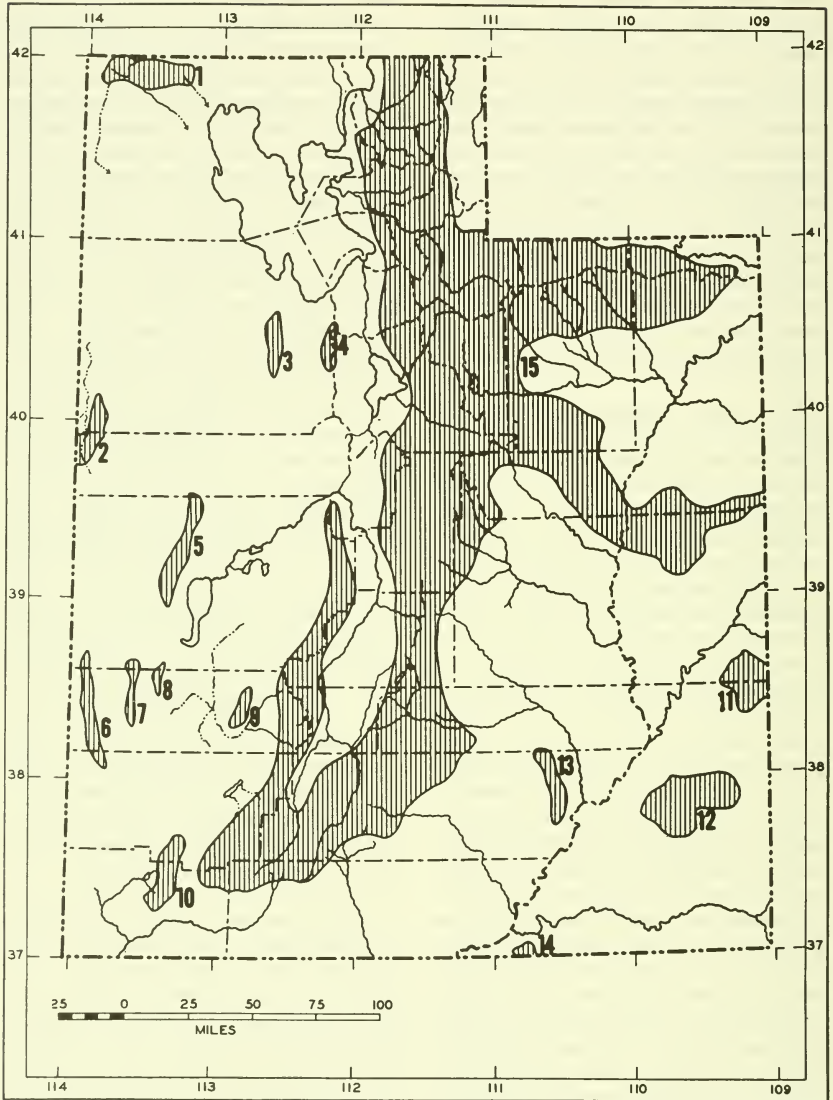


Fig. 1. Map of Utah showing locations of Boreal Islands and Rocky Mountain Continent area above 7500 feet elevation. 1. Raft River Mts., 2. Deep Creek Mts., 3. Stansbury Mts., 4. Oquirrh Mts., 5. House Range, 6. Needle Range, 7. Wah Wah Mts., 8. Frisco Mts., 9. Mineral Mts., 10. Pine Valley Mts., 11. La Sal Mts., 12. Abajo Mts.—Elk Ridge, 13. Henry Mts., 14. Navajo Mtn., 15. Wasatch-Uinta-Tushar-High Plateau Continent.

and "Standard," which occurred in 28 or more. Birds in the "Standard" category are presumed to have generalized boreal requirements in contrast to specialized requirements for the "Restricted" group. Johnson noted Willson's (1974) work that deals with aspects of habitat structure in relation to species and numbers of birds. A more recent paper along similar lines is Flack's (1976) study of bird populations in the aspen forests in western North America. The approach of Willson and Flack focuses attention on the significance of particular environmental variables presently covered by Johnson's habitat diversity score.

The next highest correlation shown by my data is with width of barrier, but this is significant only in connection with the category of permanent residents ($R = .43$). In other words, for the summer residents there is no correlation between number of kinds occurring on an island and distance from the nearest island or continent, while for the permanent residents the number of kinds decreases with remoteness from the continental area. The distance correlation is minor, however, compared with that for habitat diversity. Again my results are es-

entially the same as those of Johnson (1975). He expressed the opinion that the distance factor in the case of birds operates through impoverishment of habitat rather than through ease of access.

A low correlation shows up for my data between number of species and total area of the island (see Table 2). This is contrary to the results of both Brown and Johnson as well as the postulate of MacArthur and Wilson (1963, 1967) that area and environmental diversity are closely related and that total area serves as a good general predictor of habitat variety. The lack of correlation between number of species and size of area for the islands that I studied was probably influenced by the disparate results for the two smallest islands, namely the Frisco Mountains with a size of 11 square miles and only 19 kinds of birds as compared to Navajo Mountain with 13 square miles and 49 kinds of birds. I gave a habitat diversity score of 3 to the Frisco Mountain area and a 5 to Navajo Mountain. The Frisco range is very dry and has a sparse coniferous forest. Navajo Mountain is also lacking in surface accumulation of water, yet supports much more forest covering. Environmental

TABLE 1. Data for Boreal Islands and the Rocky Mountain Mainland in Utah.*

Area No.	Mountain Range	N ₁	N ₂	N ₃	AR	WB	DM	EHP	LHP	HDS
1	Raft River Mts.	61	22	39	64	48	79	9892	41.92	10
2	Deep Creek Mts.	52	20	32	223	9	104	12101	39.83	11
3	Stansbury Mts.	44	18	26	54	16	39	11031	40.27	8
4	Oquirrh Mts.	50	20	30	82	16	19	10676	40.22	9
5	House Range	25	9	16	25	35	63	9725	39.09	4
6	Needle Range	29	10	19	92	11	65	9783	38.16	4
7	Wah Wah Mts.	42	15	27	54	11	53	9065	38.33	6
8	Frisco Mts.	19	8	11	11	11	38	9669	38.31	3
9	Mineral Mts.	34	12	22	24	25	11	9619	38.20	5
10	Pine Valley Mts.	46	18	28	79	39	10	10325	37.32	10
11	La Sal Mts.	64	25	39	314	28	42	13089	38.26	12
12	Abajo Mts.— Elk Ridge	42	22	20	368	38	70	11445	37.50	9
13	Henry Mts.	41	17	24	108	38	21	11615	38.07	7
14	Navajo Mtn.	49	22	27	13	62	58	10416	37.02	5
15	Wasatch-Uinta Mainland	80	33	47	—	—	—	13498	40.77	18

*N₁ = total number boreal species found; N₂ = number of these permanently resident; N₃ = no. summer residents; AR = total area above 7500 feet in square miles; WB = width of interisland lowland desert barrier, e.g., distance from closest boreal island; DM = distance from mainland; EHP = elevation of highest peak; LHP = latitude of highest peak; HDS = Habitat Diversity Score.

patchiness or some other aspect of the more extensive woodland on Navajo Mountain presumably accounts for the greatly increased number of species present. In these two instances, at least, total area is not as good a predictor of number of kinds of birds as is total forest woodland area with

all the attendant attributes, whatever they may be.

From his study of boreal mammals on the mountaintops of the Great Basin ranges, Brown (1971) concluded that their diversity and distribution could not be explained in terms of an equilibrium between coloniza-

TABLE 2. Results of partial correlation analysis of island data. Upper number indicates the correlation coefficient; lower number is the level of significance. Meaning of symbols is the same as in Table 1.

	N ₁	N ₂	N ₃	AR	WB	DM	EHP	LPH	HDS
	1.000								
N ₁	.001								
	.933	1.000							
N ₂	.001	.001							
	.970	.816	1.000						
N ₃	.001	.001	.001						
	.442	.581	.313	1.000					
AR	.114	.029	.275	.001					
	.319	.428	.220	-.023	1.000				
WB	.267	.127	.449	.938	.001				
	.167	.169	.153	.329	-.018	1.000			
DM	.569	.564	.602	.251	.952	.001			
	.581	.673	.474	.771	.055	.128	1.000		
EHP	.029	.008	.087	.001	.851	.662	.001		
	.329	.145	.430	-.132	-.204	.305	-.016	1.000	
LHP	.250	.622	.125	.653	.485	.289	.956	.001	
	.867	.832	.824	.655	.091	.138	.714	.323	1.000
HDS	.001	.001	.001	.011	.757	.638	.004	.260	.001

TABLE 3. Summary of results from stepwise multiple regression analysis showing relationship of total number of bird species (the dependent variable) to independent variables. HDS = habitat diversity score; WB = width of interisland barrier; EHP = elevation of highest peak; AR = total area; DM = distance from mainland; LHP = latitude of highest peak.

Variable	Multiple R	R ²	R ² Change	Simple r
Treatment A. EHP and AR excluded as independent variables				
HDS	.86693	.75156	.75156	.86693
WB	.89979	.80963	.05807	.31877
LHP	.90712	.82286	.01323	.32918
(constant)				
Treatment B. HDS excluded as an independent variable				
AR	.44173	.19512	.19512	.44173
LHP	.58987	.34795	.15283	.32918
WB	.72392	.52405	.17611	.31877
DM	.74207	.55067	.02661	.16689
(constant)				
Treatment C. All variables included in the analysis				
HDS	.86693	.75156	.75156	.86693
WB	.89979	.80963	.05807	.31877
AR	.91085	.82964	.02002	.44173
DM	.91693	.84076	.01111	.16689
(constant)	.91870	.84402	.00326	.58097
EHP				

tion and extinction. His interpretation was that boreal mammals reached all the islands during the Pleistocene and since then there have been extinctions but no colonizations. In his study of boreal birds, Johnson (1975) concluded that a similar nonequilibrium situation prevails for the permanent resident species, but for the summer residents the equilibrium theory of island species number does apply since species are excluded by habitat deficiencies rather than barriers.

SUBSPECIES OF GEOGRAPHICALLY VARIABLE SPECIES IN UTAH

An aspect of biogeography that is of primary interest to the systematist is the geographic distribution of different subspecies

or races of geographically variable species. Twenty-three species present systematic problems in Utah. Of these, 7 are montane or boreal forms, 14 are valley or austral species, and 2 are wide-ranging types that extend from the valleys up to the mountaintops. Of the total, 14 are represented by 2 breeding races and 4 by 3 races, with possibly another in the last category. Another 4 species are represented by only one race in the state, but each has an intergrading population in some part of Utah that is transitional with another race in surrounding regions. The distribution of the races and populations in nine geographic regions in the state is indicated in Table 4 except for the Red Crossbill, about which a decision as to the number of races represented in Utah

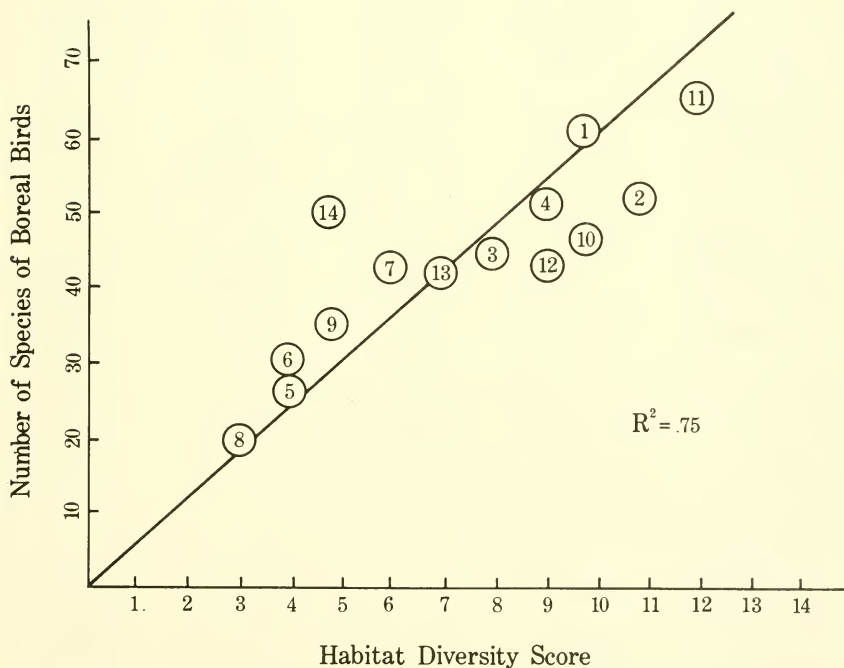


Fig. 2. Relationship between habitat diversity score (HDS) and total number of birds (N_1) occurring on boreal islands in Utah. Numbers of sample areas correspond to those used in Fig. 1 and Table 1. R^2 value shown is the adjusted value because of the small number of sample areas.

awaits the results of a pending systematic review by Allen Phillips. Areas of intergradation of varying extent occur between the races. Two instances of a minor barrier effect have been revealed. No uniform pattern of distribution prevails. Rather, there are several situations indicated whereby 2 or more species show racial changes in about the same general area. The picture of variation is more indicative of broad changes on a regional basis than of differentiation in isolated mountain ranges, as is of-

ten the case with more sedentary groups such as mammals.

One distributional pattern is where differences occur between populations in the west desert portion of northern Utah and those of the Wasatch and Uinta mountains. This is seen in the Dusky Grouse, Cliff Swallow, Mountain Chickadee, Brown Creeper, Scrub Jay, and Steller's Jay. Cliff Swallows represent an extreme case of gradual clinal variation, with only specimens from the ends of the cline in extreme western

TABLE 4: Subspecies of geographically variable birds or intermediate populations represented in various geographic areas in Utah.

	RAFT RIVER, DEEP CREEK MOUNTAINS	STANSBURY, OQUIRH MOUNTAINS	HOUSE, NEEDLE, WAH WAH MOUNTAINS	PINE VALLEY MOUNTAINS VIRGIN RIVER VALLEY BEAVER DAM WASH
<i>Buteo jamaicensis</i> Red-tailed Hawk	<i>calurus</i>	<i>calurus</i>	<i>calurus</i>	<i>calurus</i>
<i>Dendragapus obscurus</i> Blue Grouse	<i>oreinus</i>	<i>oreinus</i> > <i>obscurus</i>	—	<i>obscurus</i>
<i>Otus aslo</i> Screech Owl	<i>ingoensis</i>	<i>ingoensis</i>	<i>ingoensis</i>	<i>ingoensis</i> > <i>yumanensis</i>
<i>Bubo virginianus</i> Great Horned Owl	<i>occidentalis</i>	<i>occidentalis</i>	<i>occidentalis</i>	<i>pallascens</i>
<i>Chordeiles minor</i> Common Nighthawk	<i>hesperis</i>	<i>hesperis</i>	<i>hesperis</i>	<i>henryi</i>
<i>Picoides villosus</i> Hairy Woodpecker	<i>leucothorectis</i> > <i>monticola</i>	<i>monticola</i>	<i>leucothorectis</i>	<i>leucothorectis</i>
<i>Empidonax traillii</i> Willow (Traill's) Flycatcher	<i>adastus</i>	<i>adastus</i>	<i>adastus</i> > <i>extimus</i>	<i>extimus</i>
<i>Eremophila alpestris</i> Horned Lark	<i>utahensis</i>	<i>utahensis</i>	<i>utahensis</i>	—
<i>Petrochelidon pyrrhonota</i> Cliff Swallow	<i>hypopolia</i>	<i>hypopolia</i> > <i>pyrrhonota</i>	<i>hypopolia</i> > <i>pyrrhonota</i>	<i>tachina</i>
<i>Cyanocitta stelleri</i> Steller's Jay	—	<i>macrolopha</i>	<i>macrolopha</i>	<i>macrolopha</i>
<i>Aphelocoma coerulescens</i> Scrub Jay	<i>nevadae</i>	<i>nevadae</i>	<i>nevadae</i>	<i>nevadae</i>
<i>Parus atricapillus</i> Black-capped Chickadee	<i>nevadensis</i>	<i>nevadensis</i>	<i>nevadensis</i>	<i>nevadensis</i>
<i>Parus gambeli</i> Mountain Chickadee	<i>ingoensis</i>	<i>ingoensis</i> > <i>wasatchensis</i>	<i>ingoensis</i> > <i>wasatchensis</i>	<i>ingoensis</i>
<i>Certhia familiaris</i> Brown Creeper	<i>leucosticta</i>	<i>leucosticta</i>	<i>leucosticta</i>	<i>leucosticta</i>
<i>Catherpes mexicanus</i> Canyon Wren	—	—	—	<i>conspersus</i>
<i>Sialia mexicana</i> Western Bluebird	—	—	—	—
<i>Lanius ludovicianus</i> Loggerhead Shrike	<i>gambeli</i>	<i>gambeli</i>	<i>gambeli</i>	<i>gambeli</i>
<i>Geothlypis trichas</i> Common Yellowthroat	<i>occidentalis</i>	<i>occidentalis</i>	<i>occidentalis</i>	<i>occidentalis</i> > <i>scirpicola</i>
<i>Agelaius phoeniceus</i> Red-winged Blackbird	<i>fortis</i> > <i>nevadensis</i>	<i>fortis</i>	<i>fortis</i>	<i>fortis</i> > <i>nevadensis</i>
<i>Molothrus ater</i> Brown-headed Cowbird	<i>artemisiae</i>	<i>artemisiae</i>	<i>artemisiae</i> > <i>obscurus</i>	<i>obscurus</i>
<i>Carpodacus mexicanus</i> House Finch	<i>solitudinus</i>	<i>solitudinus</i>	<i>solitudinus</i>	<i>solitudinus</i>
<i>Melospiza melodia</i> Song Sparrow	<i>montanus</i>	<i>montanus</i>	<i>montanus</i>	<i>fallax</i>

and eastern Utah sufficiently different to be assigned to separate races (see Behle 1976a). In two species more of a step cline is represented. In one of these, the Dusky Grouse, specimens from the Deep Creek Mountains near the Utah-Nevada border, are typical of the race *Dendragapus obscurus oreinus*. Those from the Oquirrh Mountains are closest to *oreinus* but show an approach to *obscurus*. In the Wasatch Mountains the grouse represent the race *obscurus*. A similar situation exists in the Mountain Chick-

adee. Those from the Deep Creek Mountains represent the race *Parus gambeli inyoensis*. Those from the Stansbury and Oquirrh mountains are closest to *inyoensis* but show an approach to *wasatchensis* which occurs in the Wasatch Mountains and thence east to the Uinta Mountains. In the Brown Creeper, representatives from all the west desert ranges represent the race *Certhia familiaris leucosticta*. Those from the Wasatch Mountains are a highly variable lot of intergrades but as a whole stand closest

WASATCH MOUNTAINS WASATCH PLATEAU	PAVANT, TUSHAR MOUNTAINS	AQUARIUS, PAUNSAUGUNT, MARKAGUNT PLATEAUS	UINTA MOUNTAINS-- TAVAPUTS PLATEAU	LA SAL--ABAJO HENRY MOUNTAINS
<i>calurus</i>	<i>calurus</i>	<i>calurus</i>	<i>fuertesi</i>	—
<i>obscurus</i>	<i>obscurus</i>	<i>obscurus</i>	<i>obscurus</i>	<i>obscurus</i>
<i>inyoensis</i>	<i>inyoensis</i>	<i>inyoensis</i>	<i>inyoensis</i>	<i>inyoensis</i>
<i>occidentalis</i>	<i>occidentalis</i>	<i>occidentalis</i>	<i>occidentalis</i>	<i>pallescens</i>
<i>hesperis</i>	<i>hesperis</i>	<i>henryi</i>	<i>howelli</i>	<i>henryi</i>
<i>monticola</i>	<i>monticola</i>	<i>monticola</i> > <i>leucothorectis</i>	<i>monticola</i>	<i>lucothorectis</i>
<i>adastus</i>	<i>adastus</i> > <i>extimus</i>	<i>adastus</i> > <i>extimus</i>	<i>adastus</i>	<i>adastus</i> > <i>extimus</i>
<i>utahensis</i>	<i>leucolaema</i>	<i>leucolaema</i>	<i>leucolaema</i>	<i>leucolaema</i> <i>occidentalis</i>
<i>hypopolia</i> > <i>pyrrhonota</i> <i>macrolopha</i> > <i>annectens</i>	<i>hypopolia</i> > <i>pyrrhonota</i> <i>macrolopha</i>	<i>hypopolia</i> > <i>pyrrhonota</i> <i>macrolopha</i>	<i>pyrrhonota</i> > <i>hypopolia</i> <i>macrolopha</i>	<i>hypopolia</i> > <i>pyrrhonota</i> <i>macrolopha</i>
<i>woodhouseii</i> > <i>nevadae</i> <i>nevadensis</i>	<i>woodhouseii</i> > <i>nevadae</i> <i>nevadensis</i>	<i>woodhouseii</i> > <i>nevadae</i> <i>nevadensis</i>	<i>woodhouseii</i> <i>garrinus</i>	<i>woodhouseii</i> <i>garrinus</i>
<i>wasatchensis</i>	<i>wasatchensis</i>	<i>wasatchensis</i>	<i>wasatchensis</i>	<i>gambeli</i>
<i>montana</i> > <i>leucosticta</i> <i>conspersus</i> > <i>griscus</i> —	<i>montana</i> <i>conspersus</i> —	<i>montana</i> <i>conspersus</i> <i>bairdii</i>	<i>montana</i> <i>conspersus</i> <i>occidentalis</i>	<i>montana</i> <i>conspersus</i> <i>bairdii</i>
<i>gambeli</i>	<i>gambeli</i>	<i>gambeli</i>	<i>gambeli</i> > <i>excubitorides</i>	<i>gambeli</i> > <i>excubitorides</i>
<i>occidentalis</i>	<i>occidentalis</i>	<i>occidentalis</i>	<i>occidentalis</i>	<i>occidentalis</i>
<i>fortis</i>	<i>fortis</i>	<i>fortis</i>	<i>fortis</i>	<i>fortis</i>
<i>artemisiae</i>	<i>artemisiae</i>	<i>artemisiae</i>	<i>artemisiae</i>	<i>artemisiae</i>
<i>solitudinus</i> > <i>frontalis</i> <i>montanus</i>	<i>solitudinus</i> > <i>frontalis</i> <i>montanus</i>	<i>solitudinus</i> > <i>frontalis</i> <i>montanus</i>	<i>solitudinus</i> > <i>frontalis</i> <i>montanus</i>	<i>frontalis</i> <i>montanus</i>

to the race *montana*. The Steller's Jays of the west desert ranges including the Oquirrh Mountains are typical of the race *Cyanocitta stelleri macrolopha*, while those from the Wasatch Mountains constitute an intergrading population between *macrolopha* and *annectens*, a northern race. The Scrub Jays of the Oquirrh Mountains and other west desert ranges are typical of the race *Aphelocora caerulescens nevadae*, but those from the Wasatch are intergrades between *nevadae* and *woodhouseii*, closest to the latter. Thus in these several species a break occurs along the west escarpment of the Wasatch Mountains dividing west desert races from intergrading populations in the Wasatch Mountains and eastward. The Jordan Valley between the Oquirrh and Wasatch Mountains, only about 25 miles across, thus seems to act as a weak barrier for the montane forms.

The second pattern is for the break along a west-east cline to occur farther east between the Wasatch and Uinta mountains. Here there is not even a valley to serve as the line of demarcation. This situation is seen in the Red-tailed Hawk and Black-capped Chickadee. For the hawk, the population in the Wasatch and all of western Utah represents the race *Buteo jamaicensis calurus*, while those from the Uinta Basin and Tavaputs Plateau region are closest to *fuertesii*, a race which extends southeast into Texas. The Black-capped Chickadee of the Oquirrh and Wasatch ranges represents the race *Parus atricapillus nevadensis*. By the time the Uinta Basin is reached the population represents *garrinus*.

The third pattern is for a race or population to be represented in northern Utah and a different one in the southern part of the state. Exemplifying this are the Steller's Jay, Hairy Woodpecker, and Great Horned Owl. As previously noted, the Steller's Jays from the Wasatch Mountains represent an intergrading population between the races *annectens* and *macrolopha*, closest to the latter. In southern Idaho the jays are closest to *annectens*. South of Mount Nebo at the

southern end of the Wasatch Mountains, the jays are typical of *macrolopha*. In the case of the Hairy Woodpecker the break occurs south of the Aquarius, Paunsaugunt, and Markagunt plateaus. This is farther south than the transition area for the Steller's Jays. An unexpected distributional feature of the Hairy Woodpecker is that the southern race *Picoides villosus leucothorectis* extends farther north in the isolated mountain ranges of the Great Basin in western Utah than it does in the plateaus and mountains of central Utah. This suggests that the propagules for the west desert ranges came from the southeast rather than directly west from the Wasatch, a situation similar to that of the Three-toed Woodpecker (Johnson 1975: 548). Whatever the direction of spread, *leucothorectis* and *monticola* seem to have met in the Snake and Deep Creek ranges where an intergrading population occurs. In contrast, a sharp break in the distribution of the two subspecies occurs between the Tushar and Mineral mountains in southwestern Utah. The population of the Tushar Mountains is *monticola* while that of the Mineral Range about 25 miles to the west with Beaver Valley between is typical *leucothorectis*. In the case of the Horned Owls, the race extending across southern Utah is *Bubo virginianus pallescens* but its range swings north in eastern Utah to include the La Sal Mountain-Moab region.

The fourth situation is found in extreme southwestern Utah along the Virgin River Valley, where, in addition to the numerous indicator species of the Mojave Desert avifauna previously discussed, there are differences at the subspecies level for several kinds of birds. In three geographically variable species there are races that do not occur elsewhere in the state. These are a subspecies of Cliff Swallow (*Petrochelidon pyrrhonota tachina*), a race of Brown Cowbird (*Molothrus ater obscurus*), and a race of Song sparrow *Zonotrichia melodia fallax*. These three races are of southern origin. In four other species, the populations are intergradational toward southern races. This is

the case for the Screech Owl, where the population is *Otus asio inyoensis* toward *yumanensis*. The Gilded Flicker (formerly *Colaptes chrysoides* but now considered to be *C. auratus chrysoides*) has been observed in Beaver Dam Wash in Utah, and one specimen has been obtained that is intermediate between that race and the Red-shafted Flicker (*C. a. cafer*). In the Rough-winged Swallow, the population is *Stelgidopteryx ruficollis serripennis* toward *psammochroa*. In the Yellow-throat, the population is *Geothlypis trichas occidentalis* toward *scirpicola*. Yet another intergrading population occurs in the region in the case of the Red-winged Blackbird, but the race with which intergradation occurs is a western race. The population is *Agelaius phoeniceus fortis* toward *nevadensis*.

A fifth distributional pattern shows a different population in the Red Rock country of southeastern Utah as compared to the rest of the state. This is seen in the Night-hawks and Horned Larks. For the former, the race in southeastern Utah is *Chordeiles minor henryi* as opposed to *howelli* to the north in the Uinta Basin and *hesperis* in western Utah. For the Horned Larks there is an intergrading population between the race *Eremophila alpestris leucolaema* and *occidentalis* in southeastern Utah that is closest to *leucolaema*.

Finally, a situation occurs in the Horned Larks that is unlike the racial distribution of any other geographically variable species in the state. One race, *leucolaema*, occurs in subalpine meadows in the plateaus of central Utah and in alpine tundra of the Tushar Mountains, while a different race, *utahensis*, occupies the desert floor of the valleys below. The high elevation race is the same as the lowland race of the Uinta Basin in northeastern Utah. This same phenomenon of two races at different altitudes in the same general region is found in the Sierra Nevada (see Behle 1942), where the race *sierrae* occurs in montane meadows as opposed to different races in the lowland valleys both east and west of the mountains.

In contrast, in the Raft River Mountains of northwestern Utah, Horned Larks taken from the top of the mountain at 9500 feet represent the same race as in the lowlands, namely *utahensis*; and, in the Colorado Rockies, the race *leucolaema* ranges from the valleys up to the Arctic tundra at over 11,000 feet.

CLINAL VARIATION

Clines are essentially a phenomenon of geographic variation but they are also part of the picture of biogeography inasmuch as they would not be evident if samples were not present from many geographic areas. Clinal variation is manifest in the characters of many kinds of birds in the Great Basin and Utah. Occasionally similar clines appear in unrelated species, which suggests that some common environmental influence is exerting a selective influence. Clines in some instances extend in a north-south direction, while in others they extend from east to west or northeast to southwest. Phillips (1958) mentions the Song Sparrow (*Zonotrichia melodia*) in the Great Basin as an example where two clines cross perpendicularly. One cline toward longer wings and darker color extends northward while another toward short wings, large bill, and heavy breast-spotting proceeds westward. In connection with his work on the birds of Nevada, Linsdale (1938: 175) itemized the changes observed for several variable species, then generalized that for many birds there is a decrease in size toward the south. The largest individuals occur in the northeastern corner of the state. The bill becomes shorter and stubbier toward the east and smaller toward the south. The wings and tail are generally longer toward the east. General coloration becomes paler and grayer toward the east and sometimes brighter and darker in the vicinity of the Colorado River.

In Utah, clines are most evident in size characters. The usual pattern is for birds in the northern part of the state to be of

larger size than those in the southern part, with a smooth gradient occurring the length of the state. The gradient in Utah is usually a portion of a more extensive cline extending throughout western North America. A recent study that I made of the White-throated Swift (Behle 1973) revealed clinal variation nicely. Measurements of populations from Montana south to Arizona were analyzed. Clinal variation was most apparent in wing length, which is regarded in ornithological systematics as a good indicator of overall size. Clinal variation was less evident in tail length and virtually nonexistent in bill and tarsal lengths. For wing length, the means for the several populations measured showed a gradual transition from 143.2 mm in the Montana sample to 136.5 in the Arizona-New Mexico sample, a difference of 6.7 mm. While there was a general decrease in wing length from north to south in Utah samples, a mosaic pattern of variation was shown in the several semi-isolated populations represented. For example specimens from the Raft River Mountains in northwestern Utah have the longest wings in the state (average wing length 146.0 mm). They are larger than those from central northern Utah, northeastern Utah, or Colorado and are closest to the Montana population in size. Swifts from the Beaver Dam Wash in extreme southwestern Utah have the shortest wing length (wing 134.2). They are smaller than samples from central southern and southeastern Utah and are even smaller than the Arizona-New Mexico sample. These extreme Utah populations differ in average wing length by 11.8 mm, which is greater than that between Montana and Arizona-New Mexico birds (6.7 mm). The circumstance that northern swifts have longer wings than do southern swifts may be correlated with the behavioral feature that northern individuals migrate during the winter from their breeding areas while those in the southern part of their range are sedentary. Another case of north-south clinal variation in size is seen in the Cliff Swallows in western North America

(Behle 1976a). Clinal variation in size in Utah has become apparent from our studies of the Great Horned Owls and Hairy Woodpeckers (unpublished data).

Clines are also evident in Utah birds in color characters. A west-east gradient occurs in several species in northern Utah whereby paler-colored birds occur in the desert Great Basin portion of the state, with a transition eastward to darker birds in the Wasatch and Uinta mountains. Such clines are most evident in dorsal coloration. Species showing this phenomenon are the Dusky Grouse, Screech Owl, Common Night-hawk, Cliff Swallow, Horned Lark, Scrub Jay, Mountain Chickadee, and Creeper. Of the lot, the phenomenon seems to be most pronounced in the Dusky Grouse. Representatives are pale and gray in the ranges of eastern Nevada and in the Deep Creek Mountains of western Utah. In the Oquirrh Mountains they start to be slightly darker, showing more brown. The darkening is accentuated in the Wasatch Mountains and continues to a still greater degree in the Uinta Mountains and eastward into Colorado. In general, east-west clinal variation in Utah is the reverse of that for Nevada, since the birds become paler and grayer in the western part of the state, where the Great Basin occurs. Clinal variation in color from darker birds in the north to lighter birds in the south shows up in a few birds such as the Steller's Jay. In Utah, as in Nevada, brighter coloration occurs in some species in the valley of the Virgin River. Examples showing this are Yellow-throats and Song Sparrows.

SECONDARY CONTACT OF SPECIES IN THE INTERMOUNTAIN REGION

In recent years several studies have been made of secondary contact of pairs of closely related species or subspecies of birds in North America (see Selander 1965: 536, for a listing of kinds and sources of information). For most cases, the area of contact is the Great Plains, but in four instances the

phenomenon shows up in Utah. Three of these involve eastern and western kinds hybridizing. The fourth involves a northern and a southern species meeting. For two of the four the contact has probably been brought about during the past few decades; the other two are of longer duration. The first case pertains to the Indigo Bunting (*Passerina cyanea*, a species that originally occurred only in eastern North America), and the Lazuli Bunting (*P. amoena*), a western species. Apparently the planting of trees and shrubs in cities and parks across the plains states bridged the former grasslands hiatus separating the two species, and a highway was thus provided for dispersal of the Indigo Bunting westward into the range of the Lazuli Bunting. Historical records suggest that the Indigo Bunting arrived in Utah about 40 years ago. That hybridization of the two species has occurred is indicated by two intermediate specimens. One, in the Cornell University collection, was taken near Ogden, Weber County, Utah, on 12 August 1945 (Sibley and Short 1959: 447). The other is in the University of Utah collection and was taken along Minnie Maud Creek, 2 miles east of Nutter's Ranch Duchesne County, Utah, on 30 June 1966. The Indigo Bunting is now fairly common in southern Utah, where it exists sympatrically with the Lazuli Bunting. Whitmore (1975) has recently discussed the inter-specific behavioral competition now in evidence in this region between the two species.

The second instance of recently established contact in Utah pertains to two kinds of oriole, the Baltimore Oriole, formerly called *Icterus galbula*, which is an eastern type, and the Bullock's Oriole, formerly designated as *I. bullockii*, a common western kind. Worthen (1973) reported an example of the Baltimore Oriole taken 2 miles south of Milford, Beaver County, Utah, on 27 June 1964. It was one of a series of several orioles obtained at this location. Although in worn plumage, the specimen represents a "pure" first-year male. While this particular

specimen shows no tendency toward the Bullock's Oriole, some others in the series do show evidences of hybridization. Sibley and Short (1964) have shown that hybridization in the two orioles is now common throughout the Great Plains. As a result, the two orioles are presently considered as races of one species, e.g., *I. g. galbula* and *I. g. bullockii*.

The third case of hybridization in Utah pertains to flickers. There are three types of flickers in North America: the Yellow-shafted Flicker, essentially an eastern bird formerly designated as *Colaptes auratus*; the Red-shafted Flicker of the west, formerly called *C. cafer*; and the Gilded Flicker of the southwest and lower California, formerly called *C. chrysoides*. The Yellow-shafted and Red-shafted forms for over 100 years have been known to hybridize in a broad montane belt in western North America extending from British Columbia southward throughout the Rocky Mountain region. Short (1965) interprets the picture of speciation as follows. He postulates a geographic separation of the ancestral *auratus-cafer* population during the Illinois glacial age or earlier. The separation continued during subsequent periods of glaciation (except for possible hybridization between the two differentiated stocks during interglacial periods). With the waning of the last major advance of the Wisconsin period of glaciation, the eastern Yellow-shafted Flicker, *auratus*, was able to expand its range westward and northwestward into British Columbia. In contrast, the Red-shafted Flicker, *cafer*, remained restricted to the area south of the glaciers in the western United States. Eventually the two populations made contact and hybridized along the length of the Rockies. Utah is west and south of the main zone of introgression and Short scarcely mentions the area in his discussion, but there is evidence of much crossing taking place in Utah. A recent study by Rich (1967) of 137 specimens in the University of Utah collection revealed that 85 are "pure" *cafer*, 4 are "pure" *auratus*, and 48 are in-

intermediates. This is a surprisingly large number of intergrades with so few *auratus* seemingly present. It suggests that there is little or no selective pressure against the characters produced by *auratus* genes. The greatest flow of *auratus* genes into the *cafer* population pool in Utah appears to be occurring in northwestern Utah, as indicated by the highest incidence of intermediates. In contrast, there are fewer intermediates from eastern Utah, suggesting that the east-west gradient from the Great Plains area is not of great significance in Utah. In other words, the Yellow-shafted Flickers in Utah have seemingly come mostly from the northwest rather than the east. Intermediates occur throughout the Great Basin mountain ranges.

Short (1965) conceives of all the North American flickers belonging to a single species, *Colaptes auratus*, and, following his lead, the Yellow-shafted Flicker is now known as *C. a. auratus*, the Red-shafted Flicker is *C. a. cafer*, and the Gilded Flicker is *C. a. chrysoides*. The latter apparently hybridizes with the Red-shafted Flicker in extreme northwestern Arizona and southwestern Utah; Wauer and Russell (1967) report a specimen taken at the Terry Ranch in Beaver Dam Wash, Washington County, on 28 April 1965 as being a hybrid of *chrysoides* \times *cafer* derivation.

The last case of secondary contact in Utah involves two species of junco that come together in extreme northern Utah, with a relatively restricted zone of hybridization extending in an east-west direction across the state. One population is a northern form, a race of the Dark-eyed (Oregon) Junco (*Junco hyemalis mearnsi*). The other is a southern form, the Gray-headed Junco (*J. caniceps caniceps*). The contact of these two kinds was originally detected by Miller (1941: 200). At a locality 10 miles east of Kamas, all examples that he collected were pure *caniceps*. There was a shift in frequency of characters of *J. h. mearnsi* northward indicated by specimens from 20 miles north of Kamas, in the Uinta Mountains, then in

succession Woodruff, Randolph, and Garden City, until nearly pure populations of *mearnsi* were found near the Utah-Idaho border. Since then breeding hybrid juncos have been taken in the Wasatch Mountains east of Salt Lake City and in the Uinta Mountains. Hybrids extend westward in northern Utah to the Raft River Mountains and beyond into northeastern Nevada.

CENTERS OF DIFFERENTIATION IN THE GREAT BASIN

On a previous occasion (Behle 1963), I studied the distribution of the races of 50 geographically variable species of birds whose ranges include or impinge upon the Great Basin and its flanking regions. The results showed that the Great Basin is not in itself one large center of differentiation. Instead, several distribution areas were revealed that either occur in portions of the Great Basin or are situated in nearby surrounding regions. The areas were designated as the Warner Region, Sierra Nevada, Western Great Basin, Eastern Great Basin, Rocky Mountains, Northern Idaho, Inyo Region, Mojave Desert, Colorado Desert, and Navajo Country. The races of the geographically variable species occurring in each of the 10 distribution zones were listed. Since many species occupied each area, it was the different combinations of races along with common transition zones or areas of intergradation between races that served to characterize and delimit the several areas. No one species showed conformance in the distribution of its races with the various distribution areas outlined, although the horned lark approached this in slight degree. In only a few instances were races endemic in any one area. The Great Basin is too diversified in terms of environmental factors to have influenced in some common way all the geographically variable birds that are found in the region. The differentiation and distribution of the races is presumably correlated largely with localized different environments, but, in addi-

tion, barrier effects and individual histories of the various kinds of birds in terms of their point of origin, dispersal, and dependency on particular plant associations have played a role.

There are indications of three centers of differentiation in the Great Basin region, one in the eastern part, and two in the western portion. The latter two have been evaluated by Miller (1941). One is the White Mountain area of eastern California in the southwestern portion of the Great Basin. The other is the Warner Mountain-Warner Valley region of southern Oregon and northeastern California in the northwestern portion of the Great Basin. More recently Johnson (1970) presented additional data for the avifauna of the Warner Mountains and has reevaluated the affinities of the boreal elements. He gives different results than I presented (Behle 1963). The center of differentiation in the eastern part of the Great Basin rests on four races that have fairly common, though not identical, ranges. Three of these were described in the course of our fieldwork at the University of Utah, namely a race of Dusky Grouse (*Dendragapus obscurus oreinus*), a race of Horned Lark (*Eremophila alpestris utahensis*), and a race of Fox Sparrow (*Passerella iliaca swarthii*). The fourth is a race of Black-capped Chickadee (*Parus atricapillus nevadensis*) described by Linsdale of the University of California.

THEORETICAL HISTORICAL ASPECTS OF DISTRIBUTION OF BIRDS IN THE GREAT BASIN

To my knowledge, no direct evidence has been detected of the influence of Pleistocene or Holocene climates on the distribution of birds in the Great Basin or Intermountain Region. Still, some inferences can be drawn. Resident birds present in the region today are closely associated in their occurrence with particular biotic communities, especially the plant components. Since climatic change has resulted in altera-

tion of community types, the avian associates have almost certainly been affected too, either being forced out of areas where the plant habitat has disappeared or invading new areas as their requisite habitat has become established. Dispersal resulting from population pressure has also resulted in extensions of ranges. In some instances former allopatric species have become sympatric, as in the cases of the flickers and buntings. With contractions of ranges, former sympatric species conceivably have become allopatric. Such movements would be in the nature of long-term adjustments.

Of particular interest in this connection is the present-day discontinuous distribution of the coniferous forest on the mountaintops of the Great Basin and the attendant boreal species of birds. Johnson (1975: 556) has noted the two theories that have been offered to account for this. One proposes that during the Pleistocene cold climates prevailed with relatively more moisture and less evaporation than in the region today. These conditions induced the formation of glaciers in the mountains and the pluvial lakes Bonneville, Lahonton, and a host of lesser lakes on the floor of the Great Basin. At the same time, the coniferous forest presumably extended altitudinally down into the valleys, bordering on the lakes, and became distributed more or less continuously throughout the Great Basin. Boreal species of birds presumably accompanied the coniferous forest and also occurred more or less continuously at lowland elevations. Subsequent climatic change to the warmer and drier conditions of today resulted in melting of the glaciers, disappearance or diminution of the lakes, and retreat of the coniferous forest up into the mountains. The boreal birds presumably were also forced to move up into the mountains, where they occur as breeders today. Martin and Mehrlinger (1965) have mobilized the evidence from pollen studies in support of such climatic changes. In accord with this line of reasoning such avian species as the northern Three-toed Woodpecker, Water Pipit, and

Black Rosy Finch were presumably formerly much more widespread and abundant but have subsequently been confined to the mountaintops where Hudsonian zone or alpine-arctic conditions prevail. Concurrently the lowland valleys were invaded by lowland species from surrounding regions, species adapted to the warmer, xeric conditions that have come to prevail there.

The second point of view is that the montane pockets of boreal forest and attendant faunas have come about through dispersal over long distances from parental stocks such as those in the Sierra Nevada and Rocky mountains. Some evidence pertaining to the vegetation to support this interpretation has been presented by Wells and Berger (1967) and Critchfield and Allenbaugh (1967), and Johnson (1975) has noted the probable role of certain species of boreal birds such as the Band-tailed Pigeon, Pinyon Jay, and Clark's Nutcracker in long-distance colonization through transporting and/or burying seeds of conifers. In accordance with this theory, the Three-toed Woodpecker, Water Pipit, and Black Rosy Finch have extended their ranges westward from the Rocky Mountain continental area only to certain boreal islands in the eastern part of the Great Basin. Present indications are that the Rosy Finch has progressed the farthest, being known from the Jarbidge Mountains, the Ruby Mountains, and the Wheeler Peak area of the Snake Range in eastern Nevada. The Water Pipit stops at the Deep Creek Range in extreme western Utah. The Northern Three-toed Woodpecker is known from the Snake Range. However, I suspect that if more collecting were done, all three species would be found at Wheeler Peak and the Ruby Mountains in Nevada. I favor the relict mountaintop theory as Brown (1971) does for mammals. As Johnson notes, these two hypotheses are not mutually exclusive. Both processes could have occurred in the past. Extensions of range are occurring at present, as indicated by the historic record for certain species. The diversity of distribution patterns that

have been noted for Utah leads to the inference that each species has had its own particular distributional history determined by its habitat requirements and the habitat changes experienced.

MANAGEMENT IMPLICATIONS

Birds come into the picture of natural resource management in the Great Basin in several ways. In connection with environmental impact studies, special consideration is being given to threatened and endangered species such as the Bald Eagle, Peregrine Falcon, and Osprey. All of these occur in the Great Basin. Indeed, studies of raptors by Brigham Young University biologists have revealed high populations for many species in remote areas of the Great Basin. Even subspecies are important in terms of endangered species, because it is the southern race of Bald Eagle and the southern race of Peregrine Falcon that are endangered. Another area where subspecies are important in management pertains to the introduction of exotic game species. If more should be introduced (and there are serious objections to the practice) stock should be selected representing races whose native habitat is most nearly like that where the introduction is to be made. Another point is that populations at type localities, such as the Dusky Grouse (which is a game species) from the Deep Creek Mountains, should be protected. Regional avifaunistic reports, such technical papers as descriptions of new forms and systematic revisions, and symposia such as the present one, especially the published proceedings, constitute valuable resource material for those charged with making evaluations. They provide baseline data to compare against in future years to establish long-term changes.

In the 130 years since settlement of the Great Basin and other parts of the Intermountain West, many well known changes have occurred in the vegetation as pointed out by Cottam (1947) and others. Concomitant changes have occurred in the bird

life. For example, as the grassland was essentially extirpated from Utah through overutilization, the habitat for the Grasshopper Sparrow and Sharp-tailed Grouse was removed, the result being the near extermination of these kinds of birds in the region today. As pertains to the grouse, certain protected areas containing the little remaining requisite habitat are needed for its survival. One such tract is east of Wellsville, Cache County, Utah. As more and more sagebrush is removed for land cultivation, Sage Grouse and other sage-inhabiting species are being affected. The Conservation Committee of the Wilson Ornithological Society (see Braun et al. 1976) has recently reported on the extent of alteration of this community and attendant deleterious effects on the associated bird life. Chaining out of junipers and pinyon pine in the Great Basin is of less consequence in terms of the bird life because the extent of the habitat is so vast. Nevertheless, I feel that some typical areas should remain undisturbed to serve as study areas. They should be large enough to preserve habitat diversity and maintain spatial relations intact. Yet extensive areas of continuous forest may not be as effective in preserving communities and species as would numerous, smaller, diversified, irregular areas. A large, essentially undisturbed and diversified area is the Wheeler Peak region in the Snake Range in eastern Nevada. At one time the area was proposed for a Great Basin natural park. I would like to see this area so designated. This would afford some measure of protection. The Lehman Cave National Monument has already been established there. The Bureau of Land Management is, I believe, considering the designation of the Deep Creek Mountain in western Utah as a quasi-primitive area. A complication is that part of that range is Indian reservation. The Beaver Dam Wash area of extreme southwestern Utah is unique in its flora and fauna and needs protection—especially from collectors.

Regarding such theoretical considerations as the application of island biogeography

theory to conservation practice as has been advocated in the design of wildlife refuges, Simberloff and Abele (1976) express the opinion that the application of the general principle is premature at the present time. They feel that, in this particular instance, broad generalizations have been based on limited and insufficiently validated theory and on field studies of taxa which may be idiosyncratic. The implication is that much more research is needed. I suggest that the boreal islands of the Great Basin constitute propitious areas for further avian research as a sequel to Johnson's and my work.

SUMMARY AND CONCLUSIONS

Although there are no endemic species of birds in the Great Basin region of western North America, nevertheless a distinctive avifauna exists there by virtue of a different combination of birds as well as the presence of many species associated with sagebrush and the pinyon-juniper forest. Physiographic boundaries determine the limits of the Great Basin avifauna on the west and east, while on the south there is a sharp junction zone with the Mojave Desert avifauna that occurs in southern Nevada and in extreme southwestern Utah. To the north there is a gradual blending with the avifauna of the Palouse prairie and the northern montane woodland. About 30 kinds of distinctive birds that occur in the California-Pacific Coast-Sierra Nevada region are not known to occur in the Great Basin, suggesting that relatively little eastward spread has occurred. In contrast, seven Rocky Mountain species reach their western limits within the Great Basin. Some of the latter group, namely the Yellow-shafted Flicker, Baltimore Oriole, and Indigo Bunting, are recent arrivals and introgression has occurred with western congeners. Instability of present-day ranges for many species of birds is further indicated by the finding in recent years of several other kinds, mostly in southwestern Utah, that are new to the state list.

Ten northern species reach their southern

limits in at least part of their ranges in the Great Basin. A zone of hybridization between a race of the northern Dark-eyed Junco (*J. h. mearnsi*) and the southern Gray-headed Junco (*J. c. caniceps*) occurs across northern Utah and northeastern Nevada. Sixteen southern species reach their northern limits in the Great Basin, while an additional 25 species stop at a distinct Great Basin-Mojave Desert junction zone in southern Nevada and extreme southwestern Utah. Three avifaunas are represented in the Great Basin region today, namely the Rocky Mountain, Great Basin, and Mojave Desert.

Montane species, which are mostly associated with the coniferous forest, are discontinuously distributed in boreal islands on the tops of isolated mountain ranges in the general region. An analysis of the avifaunas of 14 such islands in western and southeastern Utah, as compared with that of the Rocky Mountain continent in central and northern Utah, shows a close correlation between the number of species present and habitat diversity. A slight, negative correlation shows up for permanent residents with distance from the continent. The results are similar to those of Johnson (1975) for a different set of islands mostly located in Nevada.

An analysis of the distribution of races of 22 species in Utah represented by more than one race in the state reveals a variety of patterns. For several a break occurs along the Wasatch Front on the east side of the Great Basin between a west desert race and either an eastern montane race or an intergrading population toward a different race in eastern Utah. In a few others, the break is farther east between the Wasatch and Uinta mountains. Another situation is for there to be one race in northern Utah and a different race in the southern part of the state. In three species, there are different races or populations in southeastern Utah; but southwestern Utah is the most distinctive transitional area where, in three species, different races are represented and

in five others intergradational populations occur. For the Horned Lark, one race occurs in subalpine meadows in central Utah, and a different race is a summer resident in the desert region at the base of the mountains. In some species intergrading populations occur over broad areas; in others the phenomenon is confined to a narrow zone.

A center of differentiation occurs in western Utah in the eastern portion of the Great Basin where four races of geographically variable birds have ranges that somewhat coincide. This is similar to the White Mountain and Warner Mountain centers in the western portion of the Great Basin. Clinal variation occurs in many species, involving both size and color characters. Some clines run north and south and others run east and west. Some are gradual; others are step clines. Past climatic change has doubtless influenced the distribution of species and avifaunas in the region. It is inferred that during cold intervals of the Quaternary boreal birds occurred in lowland valleys, but with a warming trend they have retreated to the mountaintops, where they are found today. This would account for the current distribution of the Water Pipit and Black Rosy Finch, although the possibility exists of a westward spread of these species from the Rocky Mountains.

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APPENDIX

Occurrence of boreal birds on montane islands and portion of Rocky Mountain Continent in Utah.

	Raft River Mts. (Behle 1958) Deep Creek Mts. (Behle 1955) Stansbury Mts. (Porter, Bushman, and Behle MS) Oquirrh Mts. (Blanchard 1973) House Range (Worthen 1968) Needle Range (Worthen 1968) Wah Wah Mts. (Worthen 1968) Frisco Mts. (Worthen 1968) Mineral Mts. (Worthen 1968) Pine Valley Mts. (Behle 1943) La Sal Mts. (Behle 1960) Abajo Mts.—Elk Ridge (Behle 1960) Henry Mts. (Behle 1960) Navajo Mtn. (Benson 1935; Woodbury <i>et al.</i> 1945) Wasatch, Uinta, High Plateaus, Tushar Mts. Continent													
*Goshawk (<i>Accipiter gentilis</i>)	X	X		X		X	X			X	X	X	X	
*Sharp-shinned Hawk (<i>Accipiter striatus</i>)	X	X	X	X	X		X		X	X	X	X	X	
*Cooper's Hawk (<i>Accipiter cooperii</i>)	X	X	X	X			X		X			X	X	
*Red-tailed Hawk (<i>Buteo jamaicensis</i>)	X	X	X	X	X		X	X	X	X	X		X	
*Golden Eagle (<i>Aquila chrysaetos</i>)	X	X	X	X	X		X		X	X		X	X	
*American Kestrel (<i>Falco sparverius</i>)	X	X	X	X						X	X	X	X	
*Dusky Grouse (<i>Dendragapus obscurus</i>)	X	X	X	X					X	X	X	X		
*Ruffed Grouse (<i>Bonasa umbellus</i>)	X												X	
*Band-tailed Pigeon (<i>Columba fasciata</i>)									X	X	X	X	X	
*Flammulated Owl (<i>Otus flammeolus</i>)				X							X		X	
*Great Horned Owl (<i>Bubo virginianus</i>)	X	X		X					X	X	X		X	
*Pygmy Owl (<i>Glaucidium gnoma</i>)													X	
*Spotted Owl (<i>Strix occidentalis</i>)												X	X	
*Long-eared Owl (<i>Asio otus</i>)			X		X								X	
*Saw-whet Owl (<i>Aegolius acadicus</i>)	X		X	X									X	
White-throated Swift (<i>Aeronautes saxatalis</i>)	X	X			X		X	X	X	X	X	X	X	

Species * = Permanent residents. Others are summer residents.

Black-chinned Hummingbird (<i>Archilochus alexandri</i>)	X				X					X			X	X
Broad-tailed Hummingbird (<i>Selasphorus platycercus</i>)	X	X	X	X	X	X		X	X	X	X		X	X
Calliope Hummingbird (<i>Stellula calliope</i>)														X
*Common Flicker (<i>Colaptes auratus</i>)	X	X	X	X	X	X	X	X	X	X	X	X	X	X
*Pileated Woodpecker (<i>Dryocopus pileatus</i>)														X
*Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	X					X	X		X	X	X	X	X	X
*Williamson's Sapsucker (<i>Sphyrapicus thyroideus</i>)												X		X
*Hairy Woodpecker (<i>Picoides villosus</i>)	X	X	X	X		X	X	X	X	X	X	X	X	X
*Downy Woodpecker (<i>Picoides pubescens</i>)	X	X	X	X						X				X
*Northern Three-toed Woodpecker (<i>Picoides tridactylus</i>)										X	X	X	X	X
Hammond's Flycatcher (<i>Empidonax hammondi</i>)	X	X	X				X			X	X	X	X	X
Dusky Flycatcher (<i>Empidonax oberholseri</i>)	X	X	X	X	X	X	X		X		X	X	X	X
Western Flycatcher (<i>Empidonax difficilis</i>)	X	X	X	X		X			X				X	X
Western Wood Peewee (<i>Contopus sordidulus</i>)	X	X	X	X					X	X	X	X	X	X
Olive-sided Flycatcher (<i>Contopus borealis</i>)	X	X					X	X		X		X	X	X
Horned Lark (<i>Eremophila alpestris</i>)	X												X	X
Violet-green Swallow (<i>Tachycineta thalassina</i>)	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Tree Swallow (<i>Tachycineta bicolor</i>)	X			X						X	X		X	X
Purple Martin (<i>Progne subis</i>)														X
*Gray Jay (<i>Perisoreus canadensis</i>)											X	X		X
*Steller's Jay (<i>Cyanocitta stelleri</i>)	X	X	X	X		X		X	X	X	X	X	X	X
*Clark's Nutcracker (<i>Nucifraga columbiana</i>)	X	X	X	X	X	X	X	X		X	X	X	X	X
*Black-capped Chickadee (<i>Parus atricapillus</i>)	X	X	X	X					X					X
*Mountain Chickadee (<i>Parus gambeli</i>)	X	X	X	X	X	X	X	X	X	X	X	X	X	X
*White-breasted Nuthatch (<i>Sitta carolinensis</i>)	X	X								X	X	X	X	X
*Red-breasted Nuthatch (<i>Sitta canadensis</i>)	X	X	X	X	X	X	X	X	X	X	X	X	X	X
*Pygmy Nuthatch (<i>Sitta pygmaea</i>)							X			X	X	X	X	X
*Brown Creeper (<i>Certhia familiaris</i>)	X	X	X	X		X			X	X	X	X		X
House Wren (<i>Troglodytes aedon</i>)	X	X	X	X	X	X	X		X	X	X	X	X	X

Rock Wren (<i>Salpinctes obsoletus</i>)	X	X	X	X	X	X	X		X	X	X	X	X	X
American Robin (<i>Turdus migratorius</i>)	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Hermit Thrush (<i>Catharus guttatus</i>)	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Swainson's Thrush (<i>Catharus ustulatus</i>)	X			X					X					X
Veery (<i>Catharus fuscescens</i>)	X													X
Western Bluebird (<i>Sialia mexicana</i>)										X			X	X
Mountain Bluebird (<i>Sialia currucoides</i>)	X	X	X	X	X	X	X	X	X	X	X	X		X
Townsend's Solitaire (<i>Myadestes townsendi</i>)	X	X		X		X	X		X	X	X	X		X
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	X	X		X						X			X	X
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	X	X	X	X	X	X	X	X	X	X	X	X		X
Water Pipit (<i>Anthus spinoletta</i>)			X							X				X
Solitary Vireo (<i>Vireo solitarius</i>)	X	X	X	X			X		X	X	X		X	X
Warling Vireo (<i>Vireo gilvus</i>)	X	X	X	X	X	X	X		X	X	X		X	X
Orange-crowned Warbler (<i>Vermivora celata</i>)	X	X	X	X			X			X				X
Virginia's Warbler (<i>Vermivora virginiae</i>)	X	X	X	X		X	X		X	X	X		X	X
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Grace's Warbler (<i>Dendroica graciae</i>)														X
MacGillivray's Warbler (<i>Geothlypis tolmiei</i>)	X	X	X	X		X	X		X	X	X	X	X	X
Wilson's Warbler (<i>Wilsonia pusilla</i>)														X
Western Tanager (<i>Piranga ludoviciana</i>)	X	X	X	X		X	X		X	X	X	X	X	X
Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)	X	X	X	X			X		X	X	X	X	X	X
Cassin's Finch (<i>Carpodacus cassinii</i>)	X	X	X	X	X	X	X	X		X	X	X		X
*Pine Grosbeak (<i>Pinicola enucleator</i>)										X				X
Black Rosy Finch (<i>Leucosticte atrata</i>)	X									X				X
*Pine Siskin (<i>Carduelis pinus</i>)	X	X	X	X	X	X	X	X	X	X			X	X
*Red Crossbill (<i>Loxia curvirostra</i>)						X	X	X	X		X	X	X	X
Green-tailed Towhee (<i>Pipilo chlorura</i>)	X	X	X	X	X	X	X		X	X	X		X	X
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)				X	X	X		X	X	X			X	X
Vesper Sparrow (<i>Poocetes gramineus</i>)	X	X								X	X		X	X

THE FLORA OF GREAT BASIN MOUNTAIN RANGES: DIVERSITY, SOURCES, AND DISPERSAL ECOLOGY

K. T. Harper¹, D. Carl Freeman¹, W. Kent Ostler¹, and Lionel C. Klikoff²

ABSTRACT.—The high elevation floras of 9 mountainous "mainlands" (3 in the Sierra-Cascade system and 6 in the High Plateau-Wasatch-Teton system) and 15 isolated mountain "islands" in the Intermountain Region have been analyzed. Mainland floras support more species per unit area and show a smaller increase in diversity as area is increased than islands. In this respect, the isolated mountains behave as true islands. The number of endemics is low on the islands (never exceeding 5 percent of any flora), however; and the island floras are overwhelmingly dominated by species with no apparent modifications for long-range dispersal. Furthermore, the eastern mainland has exerted a far greater influence on the flora and the vegetation of the islands than has the western mainland, despite the fact that the former is downwind of the islands. Thus, evidence from endemics, dispersal ecology, and sources of the floras suggests that the isolated mountains have not acquired their full floras by long-range dispersal. We conclude that although the floras of the islands have many insular characteristics, they were less isolated in the relatively recent past than at the present. The island floras do not appear to be in equilibrium in the sense that immigrations equal extinctions.

The biogeography of disjunct segments of similar habitat has intrigued biologists since the days of Charles Darwin (1859) and A. R. Wallace (1880). Their pioneering observations were based primarily on oceanic islands, but others have analyzed the biology of such habitats as caves (Culver, Holsinger, and Baroody 1973), woodlots (Curtis 1956), fresh water lakes (Barbour and Brown 1974), and isolated patches of herb land in high-elevation forests (Vuilleumier 1970).

The appeal of islandlike environments to biologists is partially explained by the fact that complete inventories of selected taxa can be prepared for several disjunct points in a reasonably short time. Furthermore, island systems are ideally suited for the analysis of such dynamic processes as dispersal, competition, and evolution. Basic principles of community structure and trophic dynamics also appear to have been better demonstrated and more easily studied in island systems than in larger, more heterogeneous environments (Lindeman 1942, Simberloff

and Wilson 1970, Brown 1971a, Heatwole and Levins 1972, and MacArthur, Diamond, and Karr 1972).

In this paper we consider the vascular plant floras of islandlike enclaves of mesic environment on high mountains in the deserts of the Great Basin. In the strictest sense, these high mountains are less isolated than oceanic islands, since dispersing propagules or their carriers may rest in the desert and survive to move on again. Also, species of the mountain islands could evolve (and apparently often have) from the floras of the unfavorable environments that separate the islands (Billings 1977). Furthermore, evidence suggests that at varying times in the Pleistocene many of the islands were connected by vegetation similar to that now confined to the slopes of the mountains (Wells and Jorgensen 1964 and Wells and Berger 1967). Nevertheless, the tops of the high mountains of the arid West provide disjunct patches of habitat that may have much in common with real islands.

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METHODS

This paper is based entirely on published floras or checklists of workers who have collected extensively on specific mountain ranges. We utilize 9 floras from the more-or-less continuous mountain systems that flank the Great Basin on the west and east and floras or checklists for 15 mountain ranges in or near the Great Basin (Fig. 1, Table 1). We have assumed that the floras of the relatively continuous flanking mountain systems (the Cascade-Sierra system in

California and the Teton-Wasatch-High Plateau system in Wyoming, Idaho, and Utah) have long had relatively free access to large floras adapted for life at high elevations and thus qualify as mainland floras in the parlance of island biogeographers.

The mountain islands have been assigned discrete boundaries which are defined by the 7500 foot contour line. The size and elevation of these islands and their distance from the mainlands were taken from topographic maps. Island-to-mainland distances were computed by summing the distances



Fig. 1. Location of the floras considered.

TABLE 1. Species diversity and physical characteristics of the study areas.

Mountain Islands	No. of Vascular Plant Species	Area above 7500 Feet (sq. miles)	Maximum Elevation (ft.)	Width of Barrier Island-Mainland (Miles)		Source of Floristic Information
				Western	Eastern	
1. Albion Mountains	220	43	10,335	153	74	Buchanan 1976
2. Cassia Mountains	107	10	8,060	145	78	Buchanan 1976
3. Deep Creek Mountains	349	131	12,101	148	106	McMillan 1948
4. East Tintic Mountains	127	5	8,218	248	14	Nebeker 1975
5. Jarbidge Mountains	422	205	10,789	126	116	Lewis 1975
6. Kaibab Plateau	400	522	9,045	285	44	MacDougall 1947
7. Pine Valley Mountains	231	79	10,325	245	9	Atwood and Higgins 1976
8. Raft River Mountains	315	64	9,892	151	57	Preece 1950
9. Ruby Mountains	471	364	11,387	92	132	Lewis 1971
10. Santa Rosa Mountains	176	48	9,779	191	200	Lewis 1976
11. Spring Range	284	125	11,918	140	114	Clokey 1951
12. Toiyabe Mountains	351	448	11,788	59	195	Linsdale et al. 1952
13. Warner Mountains	236	116	9,892	69	300	Milligan 1969
14. Wheeler Peak	305	175	13,063	142	86	Lewis 1973
15. White Mountains	486	381	14,246	8	228	Lloyd and Mitchell 1973
Mainland Areas						
16. Bryce Canyon Natl. Park	218	40	9,105	—	—	Buchanan and Nebeker 1971
17. Lassen Volcanic Natl. Park	441	27	10,497	—	—	Gillett et al. 1961
18. Mount Timpanogos	490	28	11,750	—	—	Allred 1975
19. Northern Wasatch Mountains	609	1,050	9,980	—	—	Holmgren 1972
20. Red Butte Canyon	350	1	8,235	—	—	Arnov 1971
21. Sagehen Creek Drainage	366	4	8,844	—	—	Savage 1973
22. Sequoia-Kings Canyon Natl. Park	1,082	1,014	14,495	—	—	Rockwell and Stocking 1969
23. Uinta Mountains	579	3,630	13,498	—	—	Graham 1937
24. Yellowstone Natl. Park	791	3,000	11,358	—	—	Despain 1975

across inter-island barriers of desert (areas below 7500 feet) along the shortest route possible from a particular island to the nearest edge of each mainland.

It should be noted that our island areas and distances to mainlands do not always agree with those reported by Brown (1971a), Johnson (1975), and Behle (1977), who have used some of the same islands that we have. Those discrepancies arise from the manner in which the mainland and island borders are defined by the several authors. Brown (1971a), for example, combined the White and Inyo ranges, but the flora used in our work (Lloyd and Mitchell 1973) covers only the White Mountains. Johnson (1975) let the lower edge of forest or woodland serve as the edge of his islands, while we have followed Brown (1971a) and used the 7500 foot contour as the island edge. In Johnson's (1975) work, the Pine Valley Mountains were considered to be part of the mainland, but our criteria dictate that those mountains be considered an island.

As noted elsewhere in this symposium (West et al. 1977), distance to the nearest mainland is a weak ecological variable in the Great Basin, since each mountain range has probably received migrant species from both mainlands. We measured the width of valley barrier between each mountain system and both mainlands in an effort to obtain a better understanding of the biogeographic consequences of distance.

Johnson (1975) and Harner and Harper (1976) demonstrated that habitat diversity exerts a strong influence on diversity of birds and vascular plants, respectively. Johnson (1975) used plant criteria to quantify habitat diversity for birds on Great Basin mountains, but his criteria for habitat diversity would lead to circular logic if they were used to help explain plant diversity. Conceivably, one could devise a habitat diversity measure based on physical characteristics of the sample areas, but a useful measure would probably require more information about individual mountain

ranges than is now available. Accordingly, we have used only area, elevation, and location in our analysis of factors controlling plant diversity.

The component species of each checklist have been individually considered for inclusion in our study. We have eliminated species from the checklists which are not known to occur above 7500 feet. Species that are potentially able to survive and reproduce in desert environments have also been excluded. This latter criterion was used to improve the likelihood that the islands considered are at least currently functioning as islands. We experienced difficulty in rigidly applying this last criterion, since some species which occur above 7500 feet along the eastern edge of the Great Basin do not extend above that elevation in the Sierras. We have included all species which occur above 7500 feet on the eastern edge of the Great Basin (that do not tolerate deserts) but normally occur below that elevation on the western mainland.

For each species included in the study, we have noted lifeform, likely means of dispersal, and geographic range. The lifeform categories recognized are: 1) annual, 2) perennial forb, 3) perennial graminoid, 4) shrub, or 5) tree. Categories of dispersal include: 1) megawind, 2) miniwind, 3) stick-tight, 4) fleshy fruit, or 5) no apparent modification. Species were placed in the following groups with respect to geographic range: 1) occurring on both mainlands, 2) confined to the western mainlands and a few isolated mountains, 3) confined to the eastern mainlands and a few isolated mountains, or 4) known only from one or a few mountains in this study. Because the authors of the several checklists were uneven in their treatment of taxa of subspecific rank, we have ignored such taxa.

It will be recognized that many arbitrary decisions are required to classify all of the species in respect to the foregoing characteristics. We have followed the lifeform classification given in the index of Holmgren and Reveal (1966), except that we

have separated annual plants from perennial herbs. We consider megawind propagules to be dust-like seeds (as in orchids) and seeds with large plumose appendages (as in milkweeds) that can be expected to be regularly transported over a mile by wind. Miniwind propagules are considered to include such fruits as winged utricles of some chenopods, samaras of maples, grass caryopses that have large surface-to-volume ratios, and winged seeds of conifers. Normal dispersal distance of miniwind propagules is probably no more than a few yards. The sticktight category includes "hitchhiker" fruits such as those of *Xanthium*, *Arctium*, *Circaea*, and *Bidens* which are presumably adapted for dispersal on the fur or feathers of vertebrates. Under the heading of fleshy fruits, we include drupes, pomes, berries, and fleshy cones such as those borne by *Juniperus*. We assume that such propagules appeal to and are often dispersed by birds. Propagules designated as having no modifications for dispersal are produced by a great variety of dry-fruited species in which seeds are relatively large, have a small surface-to-volume ratio, and are without wings or plumose appendages.

The categorization of individual species according to geographic range also presented difficult problems. Once the floras were recorded on computer cards, the species were separated into the four floristic groups previously mentioned. Examination of the lists thus compiled demonstrated that some of the species that supposedly occurred only on western mainlands did in fact also occur infrequently on the eastern mainlands, even though they were not encountered on any of the checklists. In like manner, some species on the list of taxa found only on checklists from the eastern mainlands are known to occur (usually sparingly) on the western mainland. Finally, species that occur on island checklists but not on mainland lists are rarely local endemics, but are instead northern or southern species or uncommon mainland species that have reached some of the isolated mountains. Despite these defi-

ciencies of the geographic range lists, we have used them for certain analyses that would have been otherwise impossible to make.

We have used Holmgren and Reveal (1966) as our nomenclatural authority for all species occurring in the Great Basin. Nomenclature of species that occur in California but do not occur in the Great Basin follows Munz and Keck (1959). Species mentioned that occur to the south of the study area but not in California are named according to Kearney and Peebles (1951) or Clokey (1951). Problems of synonymy were largely resolved with the Holmgren and Reveal (1966) checklist.

RESULTS

The Study Areas

Our floristic samples are drawn from 6 states and from areas ranging in size from 1 to 3,630 square miles. The mainland floras are distributed across a north-south gradient of about 450 miles in the west (3 floras) and 600 miles in the east (6 floras). The 15 islands are geographically centered on the Great Basin and are spread across more than 400 miles of distance in both north-south and east-west directions (Fig. 1). Maximum elevation varies from 14,495 to 9105 ft above sea level among mainland areas and from 14,246 to 8235 ft among islands (Table 1).

Unfortunately, few climatological stations are maintained at high elevations in the region. The few data that are available suggest that the climates of eastern and western mainlands are somewhat similar in respect to annual precipitation and potential evaporation at comparable elevations, while the island areas tend to receive less precipitation and to experience greater potential evaporation than either mainland. Conditions conducive to aridity appear to be maximal on the more southerly of the mountain islands considered (United States Department of Interior 1970).

The Flora

A total of 2,225 different species occur above 7500 ft elevation in the 24 floras considered in this paper. Approximately 27 percent of those species occur on both mainlands and on occasional mountain ranges between the mainlands. Some 29 percent of the species appear on the western but not the eastern mainland, and roughly 30 percent of the species are represented on the eastern but not the western mainland. The remaining species (about 14 percent) were recorded only on island checklists (Table 2).

Species representative of those occurring on both mainlands include the following:

Aconitum columbianum Nutt.
Balsamorhiza sagittata (Pursh) Nutt.
Carex aurea Nutt.
Carex lanuginosa Michx.
Elymus glaucus Buckl.
Epilobium angustifolium L.
Equisetum arvense L.
Fritillaria atropurpurea Nutt.
Geum macrophyllum Willd.
Glyceria elata (Nash) A. S. Hitchc.
Hackelia floribunda (Lehm.) I. M. Johnst.
Lonicera involucrata (Rich.) Bank
Osmorhiza chilensis Hook. & Arn.
Populus tremuloides Michx.
Pinus ponderosa Laws.
Purshia tridentata (Pursh) DC.
Ribes cereum Dougl.
Sitanion hystrix (Nutt.) J. G. Smith
Thalictrum fendleri Engelm.
Viola adunca J. G. Smith

TABLE 2. General distributional characteristics of the flora considered.

Total species	2,225
Species occurring on checklists from both mainlands	613
Species confined to western mainland or occurring on western mainland and some islands but not on eastern mainland	646
Species confined to eastern mainland or occurring on eastern mainland and some islands but not on western mainland	678
Species recorded only on islands	288

Species confined to the western mainland or that occur on the mainland and a few isolated mountains include the following:

Agropyron pringlei (Scribn. & Sm.) Hitchc.
Allium obtusum Lemmon
Artemisia douglasiana Bess.
Bromus breviaristatus Buckl.
Carex amplifolia Boott
Carex tahoenis Smiley
Cheilanthes gracillima D.C. Eaton
Cryptantha mohavensis (Greene) Greene
Hulsea brevifolia Gray
Libocedrus decurrens Torr.
Mimulus torreyi A. Gray
Oryzopsis kingii (Bol.) Beal
Pinus jefferyi Grev. & Balf.
Populus trichocarpa Torr. & Gray
Prunus emarginata (Dougl.) Walp.
Sequoiadendron giganteum (Lindl.)
Stipa californica Merr & Davy
Taxus brevifolia Nutt.
Trifolium andersonii A. Gray
Tsuga mertensiana (Bong.) Carr.

Species confined to the eastern mainland or to that mainland and a few islands are represented by the species listed below.

Abies lasiocarpa (Hook.) Nutt.
Acer grandidentatum Nutt.
Balsamorhiza macrophyllum Nutt.
Besseyia wyomingensis (A. Nels.) Rydb.
Calamagrostis scopulorum M. E. Jones
Ceanothus martini M. E. Jones
Chlorocrambe hastata (S. Wats.) Rydb.
Clematis columbiana (Nutt.) Torr. & Gray
Erigeron ursinus D.C. Eaton
Geum rossii (R. Br.) Ser.
Hierochloë odorata (L.) Beauv.
Mertensia arizonica Greene
Moldavica parviflora (Nutt.) Britton
Orthocarpus tolmiei Hook. & Arn.
Pinus edulis Engelm.
Picea pungens Engelm.
Primula parryi A. Gray
Quercus gambelii Nutt.
Ribes wolfii Rothrock
Thermopsis montana Nutt.

Species occurring on the checklists of some of the isolated mountains but on neither mainland include local endemics as well as more widespread species that penetrate our area from primarily northern or southern floras. Representatives of each of these groups are listed below.

Endemics Listed by Location

Ruby Mountain Area

- Castilleja linoides* Gray
Eriogonum kingii Torr. & Gray
Primula capillaris Holmgren & Holmgren

Spring Range

- Angelica scabrida* Clokey & Mathias
Antennaria soliceps Blake
Castilleja clokeyi Pennell
Cirsium clokeyi Blake
Opuntia charlestonensis Clokey
Penstemon keckii Clokey
Potentilla bearii Clokey
Silene clokeyi C. L. Hitchc. & Maguire
Synthyris ranunculina Pennell
Tanacetum compactum Hall

Toiyabe Mountains

- Draba arida* C. L. Hitchc.
Mertensia toyabensis Macbr.

Wheeler Peak

- Eriogonum Holmgrenii* Reveal

Species Entering from North

- Castilleja viscidula* A. Gray
Cymopterus nivalis S. Wats
Erigeron watsoni (A. Gray) Cronq.
Selaginella selaginoides (L.) Link

Species Entering from South

- Agastache pallidiflora* (Heller) Rydb.
Antennaria marginata Greene
Aquilegia triternata Payson
Arenaria confusa Rydb.
Eleocharis montana (H.B.K.) Roem. & Schult.
Festuca arizonica Vasey
Muhlenbergia wrightii Vasey

close to and well removed from the mainlands) do not differ significantly (Table 3). We had anticipated that since perennial forbs show a preference for more mesic sites (Harner and Harper 1973) and the island habitats appear to be more xeric than the mainlands, such species might be under-represented on the isolated mountains. The data lend no support to that idea. Woody species and graminoides are also uniformly distributed among the floristic groups reported in Table 3.

The number of annual species is considerably higher on the western as opposed to the eastern mainland (Table 3). In fact, if only herbaceous species are considered, Chi-square analysis demonstrates that the number of annual species on the two mainlands departs significantly from random expectations. Also, significantly fewer annual species occur in the combined flora of the islands than on the western mainland, but the island flora does not differ from that of the eastern mainland in this respect. Chabot and Billings (1972) have noted that annual species are more common in the alpine flora of the Sierras than in other alpine floras of North America.

Floristic Diversity Considerations

In respect to lifeform characteristics, the floras of the mainlands and islands (both

Species-area relationships for the total flora and various lifeform subsamples there-

TABLE 3. Lifeform relationships of the floras considered. The criterion for separation of near and far islands was a barrier width of less than or greater than 100 miles. The following four islands constitute the "far islands" category: Deep Creek, Jarbidge, Santa Rosa, and Spring. Expected numbers of species in each category (assuming random distribution of lifeform classes among floras) is enclosed by parentheses.

Floristic Group	Lifeform Class					Total
	Trees	Shrubs	Forbs	Graminoides	Annuals	
W. mainlands	27 (28.1)	111 (114.4)	696 (734.9)	226 (214.7)	181 (148.9)	1,241
E. mainlands	27 (28.4)	119 (115.4)	754 (741.4)	213 (216.6)	139 (150.2)	1,252
Near islands	30 (28.7)	108 (116.6)	776 (749.1)	204 (218.9)	147 (151.7)	1,265
Far islands	18 (16.9)	77 (68.6)	440 (440.6)	136 (128.7)	73 (89.2)	744

Summation Chi-Square = 18.285

(Not a significant departure from random expectations at 12 degrees of freedom and the 0.95 probability level.)

of are shown for both mainlands and islands in Figure 2. Three generalizations can be drawn from that figure: 1) there are consistently more species per unit area on the mainlands than on the islands, 2) floristic diversity increases faster on islands than mainlands as area increases, and 3) area usually accounts for more of the variation in species diversity on islands than on mainlands (i.e., correlation coefficients for species-area relationships are usually larger for islands than for mainlands). Observations 1 and 2 have been duplicated in numerous island biogeographic studies (MacArthur and Wilson 1967) and are commented on here only to emphasize that the isolated mountains

under study do exhibit strong similarities with true islands.

The third observation may be partially attributable to the classification of a single flora. We have treated the Bryce Canyon flora as mainland, but Figure 2 demonstrates that its flora and lifeform subsamples consistently fall on the species-area trend line for islands and well below the trend line for mainlands. Correlation coefficients for both mainlands and islands would have been improved had we classified Bryce Canyon as an island. The area lies at the southern extremity of the more-or-less continuous system of highlands extending south from northern Utah and along the western

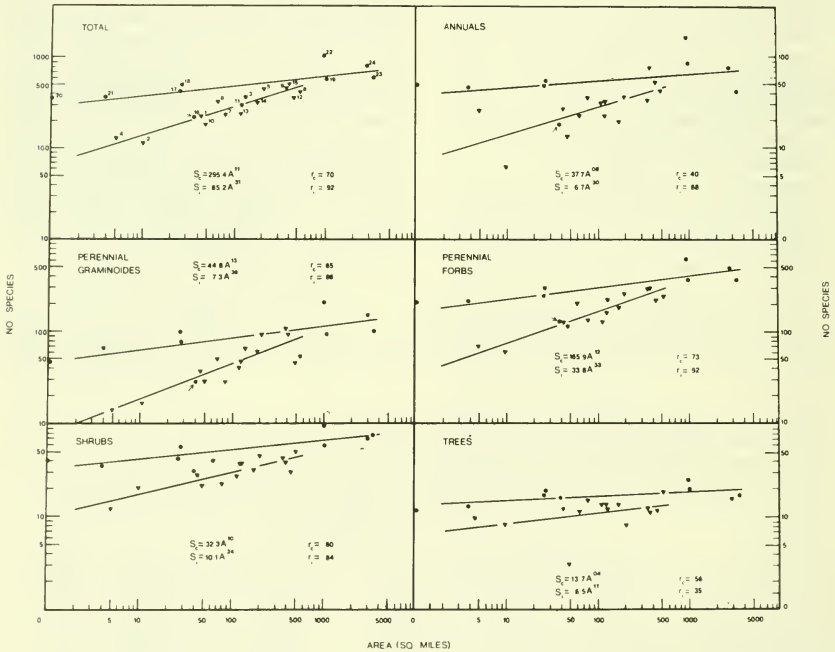


Fig. 2. Species-area relationships for mainland and island floras. Relationships for the total flora and various lifeform subsets thereof are shown. Mainland data are represented by dots; insular floras are shown with triangles. The individual floras are identified in the diagram for total species combined; numbers correspond to specific floras identified in Table 1. Subscript *c* indicates mainland correlation coefficients or regression equations; subscript *i* indicates island coefficients and equations. *S* represents number of species and *A* represents area.

edge of the Colorado Plateau. We initially considered the habitat breaks along the highland corridor to be short and inconsequential as migration barriers and thus settled on the mainland classification for the area. In retrospect, it seems likely that the narrowness of the corridor has combined with general climatic differences and unusual soils to effectively filter out numerous northern taxa that would otherwise be expected in the area.

Slopes (Z-values) for the species-area regression lines of Figure 2 are shown as the exponents of area (A) in the equations associated with the figure. The Z-value of 0.11 for total flora on the mainlands is slightly smaller than values commonly reported (e.g., 0.12–0.17 by MacArthur and Wilson 1967). The average Z-value of .19 reported for nested quadrats in pinyon-juniper ecosystems of Utah and New Mexico (Harner and Harper 1976) should probably not be compared to the Z-values obtained for mainlands in this study, since it seems likely that Z-values for nested quadrats where the largest sample area is only a few acres will always be larger than values for regional floras from areas ranging in size from a few to several hundred square miles.

The Z-value of 0.31 for the total flora of islands (Fig. 2) is well within the range of values (0.20–0.35) reported for a variety of kinds of biota on true islands and close to the theoretically expected value of 0.26–0.27 (MacArthur and Wilson 1967). We call attention in passing to the fact that woody plants have flatter species-area regression lines than perennial herbs on both mainlands and islands.

The flatness of species-area regression lines for mainlands has been attributed to the fact that small sample areas there carry individuals of many species that are poorly adapted to the sample area but nevertheless occur there because vigorous populations of each such taxon exist in nearby, suitable habitats (MacArthur and Wilson 1967). The steepness of species-area trend lines for islands is related to at least two factors: 1)

decreasing likelihood of an island being colonized by dispersing taxa as size decreases and 2) increased likelihood of local extinction of small populations on little islands.

Brown (1977) reports Z-values of 0.165 for boreal birds and 0.326 for boreal mammals on sites of isolated Great Basin mountains. He has previously reported a Z-value of 0.428 for boreal mammals, using a more restricted group of species and a different set of mountains (Brown 1971a). Our Z-value for vascular plants on isolated mountains thus lies between those for boreal birds, which seem definitely to be in equilibrium on the mountains (i.e., neither increasing or decreasing in respect to number of species per unit area over long time periods), and small boreal mammals, which are believed to be losing species by local extinction faster than new taxa can colonize. Plants in general appear to behave more like mammals than like birds on the mountains considered, and perennial herbs yield Z-values that are especially steep and approach the values reported for mammals.

Both area and maximum elevation of the mountain ranges were strongly positively correlated with total vascular species on those ranges in this study (Table 4). There was a weak negative correlation between number of species and distance to the nearest mainland. In multiple correlation analysis, only area makes a large contribution to the coefficient of multiple determination (R^2). Elevation appears to be so closely correlated with area ($r = 0.66$) that it brings little new information into the multiple correlation analysis. Distance also enters the multivariate equation; but it, like elevation, contributes only slightly over 0.01 to the R^2 -value (Table 4).

The overwhelming dominance of area in the multiple correlation analysis is, in all probability, an illusion. Wyckoff (1973) and Harner and Harper (1976) have demonstrated that both environmental favorability (annual precipitation and/or soil texture) and environmental heterogeneity (variation in soil characteristics, elevation, and/or ex-

posure) exert a strong influence on the number of vascular plant species per unit area. However, since area subsumes all of these variables, it alone consistently accounts for a highly significant amount of the variation in floral diversity in almost any suite of samples. Unfortunately, data on environmental favorability and heterogeneity are not available for the sample of mountains considered here. We have thus resorted to the use of the less definitive but nevertheless useful variables of area, elevation, and distance.

We commented earlier on the complicating effect of two close mainlands in island biogeography studies. In order to better evaluate the influence of distance between island and mainland on floristic diversity of the islands, we have measured the width of unfavorable habitat separating every island from each mainland. Then, by using only species that appear to be confined to one mainland or to one mainland and a few islands (i.e., species common to both mainlands or unique to islands were excluded), we used simple and multiple correlation to analyze the relative influence of area, elevation, and distance from mainland on the number of species from either eastern or western mainlands on the 15 islands. The results (Table 5) show that distance now becomes the major factor influencing the number of western mainland species on the islands. For eastern mainland species, distance is not significantly correlated with

number of species in simple correlation analyses, but it makes a sizeable contribution in the multiple correlation analysis. The dissimilar results for species number-distance relationships for species of western or eastern mainland origin may be related to the fact that the islands considered are on the average more distant from the western mainland (149 miles) than from the eastern (117 miles). In any event, the results in Table 5 seem to suggest that use of a single distance (distance to nearest mainland) as in Table 4 may obscure the importance of distance in studies of island floras.

We recognize also that a decrease in species of any given checklist is to be expected as one moves away from the center of the geographical area sampled for the checklist. Such a decrease with distance would be expected even in large continental areas of relatively uniform climate, topography, geological substratum, and geological history and may have nothing to do with dispersal habits of the species. The decrease may reflect nothing more than the difficulty experienced by locally evolved taxa as they attempt to expand their range through established vegetations.

Sources of the Flora

In this section we consider the question of source of the floras of the isolated mountains. How important a contribution do local endemics make to the floras of the isolated ranges? Are the island floras derived

TABLE 4. Factors influencing the number of vascular plant species on the 15 mountain islands. Distance is measured to the nearest mainland area having an elevation over 7500 ft.

Factor	Simple Correlation Coefficient (r) with Number of Species	Contribution to Coefficient of Multiple Determination (R ²)
Area of island	.879	.777
Elevation of highest peak	.668	.014
Distance to mainland	-.091	.013
		Total.799

R = .894

equally from eastern and western mainlands, or is one source more important than the other?

In respect to endemics, the data suggest that their contribution to the floras of the isolated mountains is comparatively minor. The number of endemics of moderate-to-high elevations appears to be considerably larger on the Spring Range (the Charleston Mountains which Clokey [1951] studied are part of this range) than on any other range considered here. Yet even on the Spring Range, which Clokey (1951) considered to be about five million years old, endemics account for only about 5 percent of the flora above 7500 ft. Endemics account for less than 2 percent of the White Mountain flora (Lloyd and Mitchell 1973). In contrast, plant endemics on many remote oceanic islands account for over 50 percent of the flora (Carlquist 1974). Such data force one to conclude that the mountain ranges considered are far less isolated than remote oceanic islands such as St. Helena, the Hawaiian Islands, or New Caledonia, where the majority of the flora is endemic.

In order to evaluate the relative contribution of western and eastern mainland floras to individual islands, we have separated out species unique to western as opposed to eastern mainlands (see Table 2). The relative contribution of uniquely western or eastern species on individual islands is plotted against distance to the respective mainlands in Figure 3. The data demonstrate that the eastern source area consistently contributes many more species to the islands than does the western source area. On only one island (the White Mountains) does the western mainland contribute a larger percentage of the total flora than the eastern. As will be shown later (Fig. 4), the preeminence of the eastern source area in island floras can be demonstrated for all dispersal types.

To further illustrate the relative contribution of the respective mainlands to the island floras, we have compiled a similarity matrix for all possible combinations among the 24 floras (Table 6). Various interrelationships among floras are summarized in Table 7. At first glance, the low sim-

TABLE 5. Factors influencing the number of vascular plant species on the islands when species occurring on both mainlands and on islands only are excluded. Width of barrier (distance) separating an island from each mainland has been determined for all islands.

Western Mainland Species		
Factor	Simple Correlation Coefficient (r) with Number of Species	Contribution to Coefficient of Multiple Determination (R ²)
Area of island	.502	—
Elevation of highest peak	.644	.092
Distance to W. mainland	-.646	.417
	Total	.509
	R =	.714
Eastern Mainland Species		
Factor	Simple Correlation Coefficient (r) with Number of Species	Contribution to Coefficient of Multiple Determination (R ²)
Area of island	.590	.348
Elevation of highest peak	.306	—
Distance to E. mainland	-.137	.156
	Total	.504
	R =	.710

ilarity values seem to indicate little commonality among floras, but those values must be evaluated in light of the way in which they are computed: for example, the 37 percent similarity value between the Ruby and Deep Creek Mountains represents 223 species common to those ranges. Readers are referred to the similarity equation given in the legend for Table 7 for details of computation.

Several relationships reported in Table 7 merit attention: 1) internal similarity of the floras from the western mainland is almost identical to the comparable figure for eastern mainland floras, 2) the island floras are less similar to each other than are floras from either mainland, 3) island floras are, on the average, more similar to eastern mainland floras than to western mainland floras, and 4) even islands closest to the western mainland have slightly closer floristic affinities with the eastern, rather than

the western, mainland. The second of the foregoing items indicates, as one might expect, that the flora of individual mountain islands tends to be a more random assemblage of species than is found in individual floras on either mainland. Items 3 and 4 indicate that the island floras have been more influenced by the eastern than the western mainland, despite the fact that they lie "downwind" (in this case, the prevailing westerly winds) from the western mainland. This last fact is visually conspicuous in the field since many of the dominant plants of most of the isolated mountain ranges have eastern affinities. Examples of such dominant, or at least abundant, plants include the following:

Agropyron spicatum (Pursh) Scribn. & Smith
Amelanchier alnifolia (Nutt.) Nutt.
Amelanchier utahensis Koehne
Artemisia arbuscula Nutt.
Artemisia tridentata Nutt.

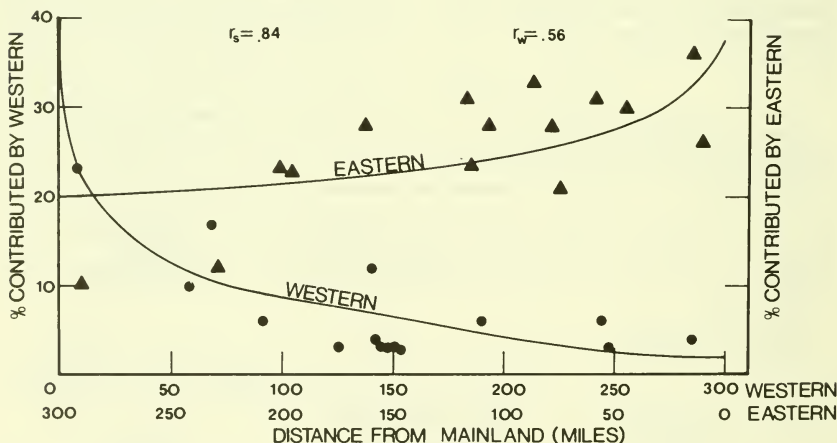


Fig. 3. Percent of the flora contributed by species that appear to have immigrated from the western as opposed to the eastern mainland. The western contribution is shown by dots, the eastern by triangles. The r_s -value represents the correlation coefficient for the curvilinear correlation between percent of species contributed by the western mainland and distance from that mainland. The r_w -value is the correlation coefficient for the curvilinear relationship between contribution of eastern species and distance (length of low elevation barrier between the islands and the eastern mainland). Individual islands can be identified in the figure by referring to island-mainland distances in Table 1.

Bromus anomalus Rupr.
Caltha leptosepala DC.
Ceanothus martini M. E. Jones
Delphinium occidentale (S. Wats.) S. Wats.
Geranium fremontii Torr.
Holodiscus dumosus (Hook.) Heller
Juniperus osteosperma (Torr.) Little
Lathyrus pauciflorus Fern.
Lewisia rediviva Pursh
Oenothera caespitosa Nutt.
Pachistima myrsinites (Pursh) Raf.
Phlox longifolia Nutt.
Primula parryi A. Gray
Ranunculus jovis A. Nels.
Valeriana occidentalis Heller

Since others (McMillan 1948 and Major and Bamberg 1967) have speculated about the relative effectiveness of northern and southern migration lanes from the western outliers of the Rocky Mountains in providing species for interior Great Basin mountains, we have investigated that problem using the similarity matrix of Table 6. Below we have summarized the relations of four interior ranges in the Basin (Deep Creek, Ruby, Toiyabe, and Wheeler Peak) with three northern sources (northern Wasatch, Mount Timpanogos, and Red Butte Canyon) and two southern sources (Bryce Canyon National Park and Pine Valley Mountains).

Mountain Range	Average Percent Similarity with	
	Three Northern Sources	Two Southern Sources
Deep Creek	31.7	21.0
Ruby	29.7	15.0
Toiyabe	25.0	18.5
Wheeler Peak	24.3	21.5

The data demonstrate that although both northern and southern routes have fed species onto the isolated mountains, the northern route seems consistently to have been more effective than the southern. The low similarity of the four interior mountain ranges with the East Tintic Mountains and their higher similarity with mountain ranges such as the Jarbidge to the north suggests that migration from the western outliers of the Rockies has been primarily along the northern rim of the Great Basin and south-

ward along the north-south-oriented mountain ranges rather than westward across the dry basins that separate the ranges of central Utah and Nevada. That hypothesis is strengthened by the low similarity shown by the East Tintic Mountains with the three northern sources (average similarity of 18 percent).

Certain species seem clearly to have reached the interior mountain islands of the Great Basin via the northern route, while others have apparently reached those islands via the southern route. Species representative of each route are noted below.

Northern Route

Ceanothus velutinus Dougl.

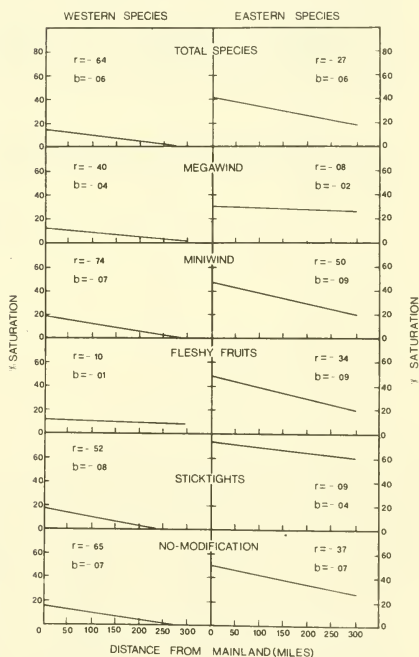


Fig. 4. Regression lines relating percent saturation of eastern or western floristic elements on the 15 islands to distance to mainland. Distance is defined as in Fig. 3. Regression coefficients (r -values) larger than .514 are significant at the 0.05 probability level. The b -values are slopes for the regression lines.

Kalmia polifolia Wang.
Ledum glandulosum Nutt.
Pinus albicaulis Engelm.
Rubus parviflorus Nutt.

Southern Route

Arctostaphylos patula Greene
Nicotiana attenuata Torr.
Peraphyllum ramosissimum (Nutt.) Rydb.
Pinus aristata Engelm.
Pinus ponderosa Laws.

Dispersal Ecology

Plant dispersal habits in both mainland and island floras are dominated by types which have no apparent modifications for dispersal and types with weak modifications for dispersal by wind (Table 8). For convenience, we refer to the latter category as the "miniwind" modification. Species whose propagules have no apparent modifications for dispersal account for from 50.4 to 53.7 percent of the species in the floras consid-

ered in Table 8. Species having miniwind propagules contribute between 28.8 and 33.5 percent of the species. Together, these two dispersal types account for almost 85 percent of the species considered. On the average, species having propagules modified for long-range dispersal by wind (megawind dispersal type) contribute almost 7.5 percent of all species in our floras. Fleshy fruited species contribute slightly fewer species (average 6.1 percent of all species), and species dispersed by sticktight contribute the few remaining species (about 2.5 percent).

Our data indicate that dispersal types modified for long-range movement (i.e., fleshy fruit and megawind categories) show no tendency to be overrepresented on the remote islands (Table 8). In contrast, Carlquist (1967) has shown that as many as 58 percent of the plant species that reach

TABLE 6. Similarity among the 24 floras as determined with the Jaccard (1912) similarity index. Values reported are percent similarity for all possible pairs of floras. Checklist numbers correspond to those assigned to each area in Table 1.

Checklist No.	Checklist No.																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1																								Albion
2	21																							Cassia
3	27	15																						Deep Cr.
4	17	11	18																					Tintic
5	28	16	32	15																				Jarbidge
6	17	11	23	13	19																			Kaibab
7	16	12	22	17	18	19																		Pine V.
8	34	22	41	18	33	20	21																	Raft R.
9	25	14	37	13	40	19	15	29																Ruby
10	26	19	21	17	30	12	14	27	23															Santa Rosa
11	14	8	23	15	16	25	22	19	17	13														Spring R.
12	20	12	29	17	28	20	20	29	27	25	25													Toiyabe
13	19	16	18	11	23	14	14	21	19	22	11	19												Warner
14	27	15	39	19	31	21	20	33	36	25	22	29	18											Wheeler
15	16	9	25	12	21	19	18	22	24	17	27	31	18	25										White
16	19	12	20	18	17	27	19	21	15	16	25	17	12	23	15									Bryce
17	14	9	17	7	23	11	13	16	21	17	12	17	23	14	17	9								Lassen
18	25	14	32	18	33	21	21	31	32	18	18	23	18	25	21	19	18							Timpanogos
19	24	14	35	15	34	24	21	32	32	18	19	28	19	25	22	18	22	47						N. Wasatch
20	26	17	28	21	32	19	22	32	25	20	17	24	21	23	16	17	17	44	40					Red Butte
21	15	12	18	8	23	11	12	16	19	15	10	19	25	15	18	9	38	18	21	17				Sagehen Cr.
22	11	6	16	6	20	12	11	14	21	10	13	18	15	14	28	9	29	17	24	15	24			Sequoia
23	21	11	31	11	31	24	17	28	30	15	18	22	17	26	20	19	17	37	39	28	16	20		Uinta
24	17	9	24	9	31	17	14	23	29	14	12	20	16	20	19	12	21	32	38	26	19	23	35	Yel

remote oceanic islands are dispersed internally by birds (mostly fleshy fruits). Propagules borne externally on birds by virtue of being held in place by barbs or prickles (sticktights) also account for many (frequently over 20 percent) of the introductions. He found windborne seeds to be poorly represented (usually less than 10 percent of the flora) on all save the closest

of the remote islands. He considered ecological conditions on the island to be strong determinants of the dispersal types that succeeded.

In contrast to Carlquist's findings, Hedberg (1970) found wind-dispersed plants to represent almost 30 percent of the flora above about 7900 ft on the mountains of east Africa. In Hedberg's study, plants dis-

TABLE 7. Floristic similarity relations among the floras considered. The index of similarity used is that of Jaccard (1912). Jaccard's index is computed as follows:

$$SI = \frac{C}{A + B - C} \times 100.$$

In the equation, C represents the number of species common to the two floras, A is the number of species in flora A, and B is the number in flora B.

Areas Considered	No. of Floras Involved	No. of Comparisons Averaged	Average Percent Similarity
Western mainland (internal similarity)	3	3	30.3
Eastern mainland (internal similarity)	6	15	30.1
Mountain islands (internal similarity)	15	105	21.0
W. mainland compared with islands	18	45	15.0
E. mainland compared with islands	21	90	21.4
W. mainland compared with E. mainland	9	18	17.3
Four closest islands to W. mainland compared to W. mainland	7	12	18.1
Four closest islands to W. mainland compared to E. mainland	10	24	18.8
Four closest islands to E. mainland compared to W. mainland	7	12	11.4
Four closest islands to E. mainland compared to E. mainland	10	24	21.0

TABLE 8. Plant dispersal habits of the floras considered. Expected number of species in each category (assuming random distribution of lifeform classes among floras) is enclosed by parentheses. Island groups are defined as in Table 3.

Floristic Group	Mega- wind	Mini- wind	Fleshy Fruits	Stick- tights	No Modification	Total
W. mainland	93 (92.3)	358 (395.8)	88 (75.3)	36 (30.9)	666 (646.7)	1,241
E. mainland	104 (93.2)	414 (399.3)	77 (75.9)	26 (31.1)	631 (652.4)	1,252
Near islands	83 (94.1)	415 (403.5)	65 (76.7)	30 (31.5)	672 (659.2)	1,265
Far islands	55 (55.4)	249 (237.3)	43 (45.1)	20 (18.5)	377 (387.7)	744

Summation Chi-Square = 15.501

(Not a significant departure from random expectations at 12 degrees of freedom and the 0.95 probability level.)

persed internally by birds accounted for only 1 to 2 percent of the alpine flora of east Africa.

The relationship between various dispersal types and island-to-mainland distance is presented in Figure 4. There, we regress percent saturation of species of various dispersal habits (i.e., the number of species of a given dispersal habit on each island is expressed as a percentage of the number of species of that dispersal habit that would be expected in an area of comparable size on the appropriate mainland) against distance. As expected, the regression lines all have negative slopes, and there is a slight (but statistically nonsignificant) tendency for dispersal types that are easily dispersed over long distances (megawind and fleshy fruit types) to have regression lines with gentler slopes than are obtained for species that are less likely to be dispersed far from the parent plant. Average slope values for western and eastern mainlands and each dispersal type are shown below.

Dispersal Type	Average Slope Value
Megawind	.03
Fleshy Fruits	.05
Miniwind	.08
Sticktight	.06
No Modification	.07

The data in Figure 4 also support our earlier conclusion that the eastern mainland has exerted a greater influence on the mountain islands than has the western mainland. Every dispersal type shows greater saturation for eastern species than for species from the western mainland. Since the number of species originating from each of the two mainlands is roughly equal (see Table 2), the results in Figure 4 suggest that species from the eastern mainlands have been about four times as effective in reaching and surviving on the islands as those from the west. On the average island, western species have a saturation value of 8 percent, but the comparable value for species from the eastern mainland is 36 percent.

The great disparity between correlation coefficients for saturation-distance analyses for eastern and western species in Figure 4 is noteworthy. In five of the six analyses the *r*-values are much larger for western species. It seems possible that those values reflect a differential in age of the two floristic elements on most of the islands. If the Rocky Mountains are much older than the Sierras, as Billings (1977) reports, it is possible that the eastern floristic element has dispersed essentially to its limit and is now poorly related to distance, while the western element is still actively dispersing.

Finally, we call attention to a conspicuous relationship between range limits of species and plant lifeform. Our data demonstrate that woody plants and perennial graminoid species are overrepresented in the broad-range category (i.e., occurring on both mainlands) and underrepresented in the category of species unique to islands (Table 9). Perennial forbs, on the other hand, display a significant tendency toward underrepresentation in the broad-range category and overrepresentation in the island-only class. Annual species show no significant trends in this respect. It seems possible that the patterns observed reflect evolutionary rather than dispersal processes. In general, woody plants and graminoides appear to be ecologically broad niched and to have the ability to become community dominants. In contrast, many perennial forb genera seem to be narrow niched and to rarely achieve a dominant place in their community.

DISCUSSION

Mountains as Islands

One might expect an island flora to be distinguished from that of the nearest mainland in a variety of ways. As we began this study, it seemed to us that insular floras should display 1) an overrepresentation of species modified in one way or another for

long-distance dispersal, 2) fewer species per unit area than observed on the mainland, 3) steeper species-area curves than for mainland floras, 4) uneven stocking of species ecologically preadapted for existence on available islands, and 5) higher rates of endemism than the mainland.

Our results demonstrate that the isolated mountains of the Intermountain West satisfy some of our preconceived notions and thus qualify as islands, but they fail to qualify on other counts. The islands do indeed have fewer species per unit area than adjacent mainlands, and species-area trend lines for islands are steeper than those for mainlands (Fig. 2). Although the amount of endemism is low on the islands (always less than 5 percent), the amount still appears to be higher than on areas of comparable elevation and size on the mainlands. Too, there is uneven stocking of species on the islands. The Pine Forest Mountains of extreme northwestern Nevada, for example, are stocked by *Pinus albicaulis* Engelm., the Santa Rosas by *Pinus flexilis* James, while the Jarbidge and Ruby Mountains to the east and the Sierras to the west have both. The observed distribution pattern for these and many other species [e.g., *Abies concolor* (Gord. & Glend.) Lindl. and *Picea engelmannii* Parry ex Engelm.] seems explainable only in terms of randomness of colonization

and/or extinction (See Critchfield and Allenbaugh 1969 for range details for these and other conifers in the Great Basin.)

Our expectations relative to an overrepresentation of species modified for long-range dispersal on the islands in large part failed. The isolated mountains are overwhelmingly dominated by species with no obvious means for being dispersed great distances. Furthermore, there is no tendency for species with modifications for long-distance dispersal to be overrepresented on even the most distant islands (Table 8). Our data do, however, show a weak tendency for percent saturation of poorly dispersed species (i.e., no-modification, miniwind, and sticktight categories) to decline faster and more reliably (larger *r*-values) with distance than for megawind and fleshy-fruited species, which are probably more easily dispersed (Figure 4).

Recent literature references demonstrate that at least some of the species that we have classified as unmodified for dispersal are, in fact, highly adapted for dispersal by vertebrate animals. Although we placed all conifers with unwinged seeds in the unmodified-for-dispersal category, a recent paper by Vander Wall and Balda (1977) shows that the Clark's Nutcracker regularly disperses the seeds of several pines (*P. edulis*, *P. albicaulis*, and *P. flexilis*) in a sublingual

TABLE 9. Plant lifeform relative to the range limits of the species considered. Expected number of species appears in parentheses in each category.

Range Category	Lifeform Class				Total Species
	Woody Plants	Perennial Herbs Forbs	Graminoides	Annuals	
Occurring on both mainlands	94 (70.0)	333 (368.6)	114 (98.9)	72 (75.5)	613
Occurring on one mainland only	140 (151.1)	795 (796.2)	215 (213.6)	174 (163.0)	1,324
Occurring on islands only	20 (32.9)	210 (173.2)	30 (46.5)	28 (35.5)	288

Summation Chi-Square = 36.020**

(A significant departure from random expectations at 6 degrees of freedom and the 0.99 probability level.)

pouch and caches them in soil suitable for their germination and growth. In addition, the Nutcracker is known to occasionally feed on the winged seeds of *Pinus aristata* and *Pinus ponderosa* in northern Arizona. Vander Wall and Balda (1977) have evidence for the dispersal of seeds over 13 miles in a single flight by the Nutcracker. In California, the Nutcracker regularly feeds on and caches the seeds of *Pinus monophylla* Torr. & Frem. and *Pinus jefferyi* as well as *Pinus albicaulis* and *Pinus flexilis* (D. Tomback, personal communication). Johnson (1975) suggests that the Piñon Jay and the Band-tailed Pigeon may also be involved in long-distance transport of coniferous tree seed. J. Pederson (personal communication) reports that the Band-tailed Pigeon has been taken several miles from the nearest *Quercus gambelii* in southeastern Utah with a crop full of unbroken acorns. Staniforth and Cavers (1977) demonstrate that some seeds of two *Polygonum* species (*P. lapathifolium* L. and *P. pensylvanicum* L.) retain viability after passing through the digestive tract of the cottontail rabbit in eastern Canada. The foregoing data lead us to suspect that large seeds from the dry fruits of many species will eventually be shown to be dispersed by vertebrate animals.

The foregoing discussion is an acknowledgement that we have underestimated the number of plant species that are modified for long-range transport on our islands. Nevertheless, the number of species in the no-modification and miniwind categories is so great on the islands that we are still forced to conclude that the vast majority of the species there did not reach those sites by long-range dispersal. Although the high elevation community types may never have been able to survive on the valley floors at any time during the Pleistocene, as Wells and Berger (1967) argue, many of the community components may have been able to migrate directly across valley floors during that period. Also, as Billings (1977) emphasizes, climatic cooling would have signifi-

cantly narrowed the barriers between islands.

Our discussion of mountains as islands would not be complete without some comment on the question of equilibrium of species number on the islands. Brown (1977) contends that birds and small mammals are not in equilibrium on isolated mountains in our study area. Are the plants in equilibrium? It will be recognized that the equilibrium argument is based on two assumptions: 1) local extinctions do occur, and 2) new introductions occur as often as extinctions on each island. Both assumptions are difficult, if not tactically impossible, to test conclusively. A definitive test would require that we know of every population of every species on every island, and that we monitor each island regularly enough (preferably annually) in order to know when a species became extinct or immigrated and became established there. Obviously, such data are not available for any island in our study. As a consequence, any statement about the status of our islands relative to the equilibrium question must be based on inferences, not facts.

With respect to extinctions, there is conclusive evidence that *Pinus aristata* and *Pinus flexilis* coexisted with *Abies concolor* and *Juniperus osteosperma* on Clark Mountain in southeastern California about 25,000 years ago (Mehring and Ferguson 1969). Today neither of these pines occurs there. Similarly, *Pinus monophylla* and *Juniperus osteosperma* existed on the Turtle Range 14,000 years ago (Wells and Berger 1967), but do not occur there now. The relatively steep species-area curves for herbs (Fig. 2) may indicate extinctions, but we can offer no evidence in support of that possibility.

Concerning new immigrations onto the isolated mountains, there are abundant records of exotic species invading at lower elevations (Young, Evans, and Major 1972). Nevertheless, we know of no documented cases of unaided immigrations onto the mountains of species that cannot survive in at least some microsites on the valley floors.

There is strong evidence that species modified for long-range dispersal are not overrepresented on the islands relative to the mainlands (Table 8). If extinctions and immigrations had been in equilibrium, even since the close of the Pleistocene, one might have expected long-range dispersal types to be at least somewhat overrepresented on islands; but even that tendency is not observed (Table 8). As noted above, there is a weak tendency for percent saturation of long-distance dispersal types to decline less rapidly against distance from the mainland than for supposedly less well-dispersed taxa. These two bits of evidence lead us to tentatively conclude that the flora of the isolated mountains is not in equilibrium, even though some species do appear to be moving about in the area.

If the islands are not in equilibrium, the extinction rate must be low for all plant groups and especially so for the woody taxa. We draw this inference from the relative flatness of the species-area curve for most plant groups (Fig. 2) in contrast to mammals (Brown 1977). Intuitively, this inference seems valid since herbaceous plants as primary producers should be able to maintain larger populations than their vertebrate consumers. Woody plants (especially trees) would be expected to maintain smaller populations than their vertebrate consumers, but would have far greater longevity. Trophic position and longevity likely have much to do with the relative extinction rate of vertebrates and plants. Plant groups of differing trophic habit (e.g., vascular saprophytes and nongreen parasites such as *Corallorhiza* and *Orobancha*, respectively, versus photosynthetic forms) and longevity should show different extinction rates.

We had not expected to find the eastern mainland (Rocky Mountains) floristic element to be so much more successful than the western mainland (Sierra) element on the Great Basin mountains. As others have noted in this symposium, the Rocky Mountain element also dominates the avian fauna (Behle 1977 and Johnson 1977) and the al-

pine flora (Billings 1977) of the isolated mountains. The evidence seems to imply that three basic factors have combined to give the Rocky Mountain element an advantage over that from the Sierra. Those factors are: 1) time, 2) geological parent material, and 3) climate.

As Billings (1977) has noted, most of the Great Basin mountains are younger than the Rockies and older than the present Sierra Nevada and Cascade ranges. Thus, species from the east have had longer to colonize the isolated mountains than high-elevation taxa from the Sierra, since that flora must have arisen much later than the first. In addition, propagules of species unique to the western mainlands would have had great difficulty establishing themselves on the mountain islands even after reaching them, since most habitats would have already been occupied by eastern taxa.

Plants originating at higher elevations on the western mainland could generally be expected to be adapted to acidic soils, since the Sierra Nevada is primarily composed of acidic, igneous rock (Major and Bamberg 1967). Soils on the isolated Mountains, however, have prevailingly basic to circum-neutral soils. Again, taxa from the eastern mainland would have an advantage in colonizing the islands, since the western outliers of the Rockies are prevailing formed from calcareous rocks. In this connection, it is significant that Billings (1950) found assemblages of Sierra plants in the western Great Basin to be confined to acidic habitats on hydrothermally altered rocks.

Finally, western plants have evolved in an environment that is less continental (i.e., more moist and thermally less variable) than that associated with the isolated mountains of concern or the western outliers of the Rockies. Johnson (1977) considers the climatic variable to be highly influential in confining western bird species to the Sierras. We believe that continentality may similarly increase the difficulty of establishment of western plant species that are dispersed to the mountain islands. As in the

preceding cases, species from the east would be better preadapted for life on the islands.

Niche Expansion

Brown (1971b) has shown that the altitudinal range of a normally low-elevation chipmunk (*Eutamias dorsalis*) expands upward on Great Basin mountains which lack a high elevation congener (*E. umbrinus*). In the course of our work on isolated mountains in the Region, we have observed several cases in which plant species also display a niche expansion in the absence of normal competitors. Although quantitative data are lacking, we take this opportunity to put such anecdotal evidence as is available on record.

An apparent case of niche expansion is presented by *Abies lasiocarpa* in the Jarvis Mountains. There, in the absence of its common coniferous competitors (e.g., *Abies concolor*, *Picea engelmannii*, *Picea pungens*, and *Pseudotsuga menziesii* (Mirb.) Franco), *Abies lasiocarpa* plays a major role in forest vegetation from the sagebrush-grass and streambank communities at low elevations to timberline. We know of no other place where this species succeeds in such a variety of habitats.

A double zone of *Artemisia tridentata* occurs on mountainsides of Nevada and western Utah. There the species commonly dominates a wide belt both below and above the juniper-pinyon zone. It appears likely that *Artemisia* has simply moved into a zone that is elsewhere dominated by larger mesophytes such as *Quercus gambelii*, *Pinus ponderosa*, or a rich mixture of mountain brush species.

In the northern Wasatch Mountains, the range of *Acer grandidentatum* extends many miles farther north than that of its common associate in the south, *Quercus gambelii*. In mixed stands of *Acer* and *Quercus*, *Acer* is normally conspicuous only on slope bases and ravine edges. North of the limits of *Quercus*, however, *Acer* dominates both slopes and depressions. The phenomenon

can be seen with particular clarity in the southwest corner of Cache Valley, Utah.

Although *Chamaebatiaria millefolium* (Torr.) Maxim. occurs on both of the mainlands recognized in this study, it is rarely a conspicuous component of the vegetation on either. On the remote islands, however, *Chamaebatiaria* is often common and a conspicuous part of the vegetation.

Finally, West et al. (1977) review evidence suggesting that the anomalously high upper elevation of the juniper-pinyon zone on many of the isolated mountains of the Great Basin may be attributable to the low diversity of the high-elevation flora and the paucity of well-adapted competitors. They note also that the niche of both juniper and pinyon appears to be severely compressed on the west flank of the southern and middle Wasatch Range where *Quercus gambelii* and *Acer grandidentata* combine to form a dense woodland. Both juniper and pinyon occur in the flora there, but neither is an important part of the vegetation.

Adequacy of Checklists

In the inception of this study, we were concerned that the checklists on which our work would be based would be too incomplete to give meaningful results. In retrospect, we acknowledge that all of the lists are probably incomplete. Undoubtedly, additional effort will add a few species to some lists and many to others. Nevertheless, the lists have yielded results that seem reasonable and defensible. Furthermore, the sample on hand is already sufficiently large to minimize the possibility that new collections will seriously alter species-area relationships or lifeform and dispersal-type spectra for the floras.

Management Implications

Species-area curves reveal much that should be useful to natural resource managers. The curve for trees on islands in Figure 2, for example, suggests that the Santa Rosa Mountains are drastically understocked with trees. Could trees be successfully in-

roduced there to provide shelter for animals or construction materials for man? Since other islands in the study support so many more tree species than that range, we suspect that introduction of one or a few carefully selected tree species into favorable sites would have a high probability of success there.

Species-area curves also have many useful implications for conservation programs for unusual and rare plant and animal species. Managers will find the basic theory relative to rare species and size of reserves nicely capsulized in the following short, non-technical papers: Terborgh (1974 and 1976), Diamond 1976, Whitcomb et al. (1976), and Simberloff and Abele (1976).

Johnson (1975) developed a habitat diversity index that accounted for a major portion of the observed variation in number of bird species on isolated mountains in the Great Basin. Behle (1977) has verified that the index is a useful indicator of bird diversity throughout the Basin. Since that index is based on various plant parameters and the presence or absence of free flowing water, it has relevance to our discussion here. Many of our small, arid mountain ranges in the Intermountain West have only a few acres of complex forest habitat (a prime variable in Johnson's index) in a single location and but a few score feet of flowing water. Since the index shows that bird diversity is highly dependent upon such habitat, it would seem prudent for developers interested in preserving the natural biotic diversity of the environment to insure that roads, campgrounds, or buildings not infringe upon such habitats. Yet, unfortunately, our developments often are centered directly on such microenvironmental rarities. By so locating developments, we almost insure that we will lose some and perhaps many plant and animal species from the entire range. The campground at Blue Lake on the Pine Forest Range in northwestern Nevada is a prime example of such faulty planning. With foresight, the development could have been placed well away

from the lake but still in the open pine groves. Water could have been piped to the campground with minimal disturbance to the natural system around the lake. Instead, the current plan places every visitor in a position to disturb the several unusual plant and animal species that perhaps occur at only that spot on the entire range.

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ALPINE PHYTOGEOGRAPHY ACROSS THE GREAT BASIN

W. D. Billings¹

ABSTRACT.—Alpine vegetations and floras are compared in two transects across the Intermountain Region. The first extends from the Beartooth Mountains in the central Rocky Mountains to the central Sierra Nevada some 1200 km to the southwest. It includes six mountain ranges. The second transect crosses the Mojave Desert from Olancha Peak in the southern Sierra Nevada to Charleston Peak and thence to San Francisco Peaks in northern Arizona. The largest numbers of arctic-alpine species are in the Beartooth and Ruby mountains, indicating migrations of these species along the Rocky Mountain cordillera. The lowest numbers of arctic-alpine species are in the central and western Great Basin and in the Sierra Nevada. Sørensen's Index of Floristic Similarity was calculated for all possible pairs of the nine alpine areas. There is little correlation of floristic similarity with alpine proximity across the Intermountain Region. Rather, any such correlation seems to be in a north-south direction; this is stronger in the eastern part of the region. Insularity and uniqueness of alpine floras seem to increase toward the western part of the basin. This is probably due to evolution of alpine endemics from preadapted low-land taxa.

The middle-latitude mountains of North America north of Mexico, for simplicity and convenience, may be grouped into four large systems. With few exceptions, the mountains in these systems trend north to south, a fact of considerable importance in the phytogeography of arctic and alpine plants. The four systems are the Appalachians in the eastern part of the continent, the Rocky Mountains, the Cascades-Sierra Nevada, and last, but not least, the Great Basin ranges. The latter three systems dominate the western third of the continent.

In general, the mountain ranges, in their present forms, are younger the closer they are to the Pacific Coast. The Appalachians constitute a very old mountain complex dating from Permian and Triassic times. Much of the large Rocky Mountain system originated in the Laramide Revolution in late Cretaceous and early Paleocene. The oldest basin ranges also rose during the Laramide Orogeny, but most of these ranges, particularly in the west, have been upthrust during a period of time from the Oligocene to the Pleistocene. Additionally, the whole basin

floor has been uplifted in the Pleistocene. Orogenic activity continues at present. Even though the Sierran batholith is rather old, the present Sierra Nevada is primarily a product of uplift during the Pliocene and Pleistocene (Axelrod 1962 and pers. comm. 1973; Bateman and Wahrhaftig 1966). Fossil lobed oak leaves at 2850 m in the lower alpine zone on Elephant's Back, south of Carson Pass, lend additional evidence of recent Sierran uplift. The high volcanoes of the Cascades are also of similarly recent age.

ALPINE ISLANDS IN THE GREAT BASIN

There are some 200 individual mountain ranges within the Great Basin. Most of these trend in a general north to south direction and are separated by broad desert valleys. In the days when mountain ranges were shown on maps by hachures, Dutton described the pattern as similar to an "army of caterpillars marching to Mexico" (Morrison 1965). These basin ranges, with elevations which vary from about 1800 m to over 4300 m, are by no means alike either

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geologically or botanically. Holmgren (1972) divided the region, on the bases of floristics and geology, into four main divisions made up of 16 sections. The mountain ranges within any one section have certain characteristics in common but also there are some rather remarkable ecological differences between mountains within the same section. Holmgren notes that there is greater variation in floristic composition of the alpine zone across the Great Basin from one peak to another than occurs in any other zone. I agree.

For many years, biogeographers working in mountain areas have compared isolated mountain ranges and summits to islands (Wallace 1880, Willis 1922). With increased interest in island biogeography (MacArthur and Wilson 1967), several important papers have appeared which provide quantitative information on the geographical relationships among the biota on isolated montane "islands." Notable among these are those of Hedberg (1970) on the Afroalpine floras, F. Vuilleumier (1970) on páramo avifaunas of the northern Andes, B. S. Vuilleumier (1971) and Simpson (1974) on páramo floras, Brown (1971) on mountaintop mammals in the Great Basin, and, recently, Johnson (1975) on bird species on montane islands in the Great Basin. MacArthur (1972) also carried his theory over to montane islands in the Appalachians in his study of the distributions of thrush species. It is notable that two of these papers (Brown's and Johnson's) are concerned with the islandlike distribution of vertebrates in the Great Basin. Nor have plant geographers ignored the island nature of the Great Basin montane islands (P.V. Wells, pers. comm. July 2, 1968, and, of course, Harper et al. in this symposium).

Both Brown and Johnson have viewed the Great Basin desert "sea" and its montane islands as being bordered on the east and west by large cordilleras, the Rocky Mountains and Sierra Nevada, which they designate as "mainlands" or "continents." The desert sea is open to the south as far as the real sea off Mexico. However, to the north,

the desert sea eventually diminishes until it is blocked by the jumbled mountain masses of British Columbia which connect the coastal mountains and the Rockies.

Johnson (1975) used the lower edge of forest-woodland as the perimeter of his islands. This is a real biological boundary. On the other hand, Brown (1971), Harper et al. (this symposium), and I have defined the lower boundaries of the montane islands rather arbitrarily. Harper et al. and Brown have used an elevation of 7500 ft (2286 m) while I have used 9000 ft (2743 m) as an approximation of the extreme lower elevation of alpine plants (Fig. 1). This latter figure is a somewhat liberal estimate of the lower limits of alpine islands in the Intermountain Region, but some alpine sites do exist this low, particularly in cirques. Timberline is usually higher than this and is often very ragged at its upper limits. Upper timberline is frequently used as the boundary between subalpine and alpine vegetation in North America. However, on most mountains of the earth it is not a particularly good boundary, and it is not a good boundary on most American mountains either, including those of the Great Basin. Timberlines almost always exist at much higher elevations than the lowest patches of alpine vegetation. This is often true around glacial valleys, both those with and those without glaciers at the present time. For example, timberline around the Athabaska Glacier in the Canadian Rockies is fully 675 m above the terminus of the glacier, where in the morainal gravels there are a number of arctic-alpine plant species but no trees. The reasons for this ubiquitous phenomenon are rather simple: those factors which define the lower limits of alpine species are not necessarily those which limit the upward distribution of trees.

As Figure 1 indicates, even conservative alpine islands in the Great Basin are much smaller and more isolated from each other than the mountain ranges themselves. But these alpine islands have been both larger and smaller in the past than they are at

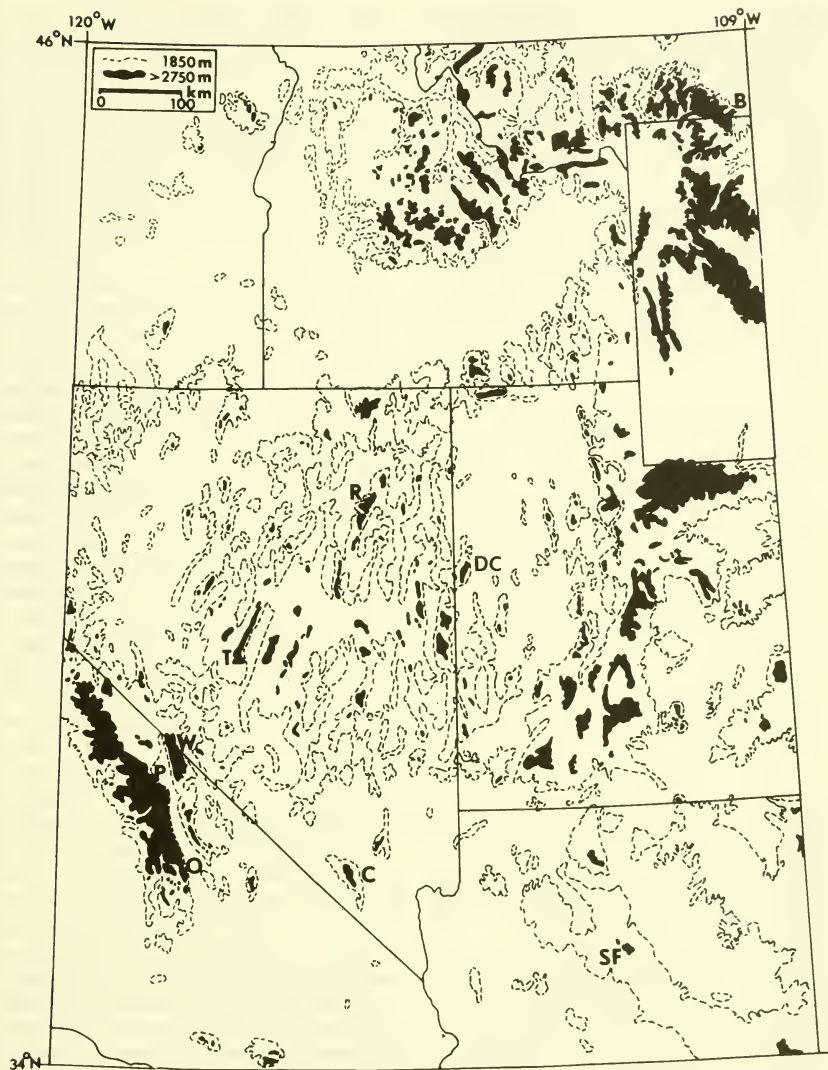


Fig. 1. Map of the Intermountain Region showing, in black, areas above 2750 m in elevation. These represent areas which are wholly or partially "alpine" at the present time. The dashed line at the 1850 m contour is an approximate estimate of what could have been the lower limit of alpine vegetation at full-glacial. Alpine regions used in the northern transect are indicated from left to right by letters: P, Piute Pass (Sierra Nevada); W, Pellissier Flats (White Mts.); T, Toiyabe Mts.; R, Ruby Mts.; DC, Deep Creek Mts.; B, Beartooth Mts. Those in the southern transect are: O, Olancho Pk and two nearby peaks in the southern Sierra Nevada; C, Spring Mts. (Charleston Peak); and SF, San Francisco Peaks.

present. The areas of such islands during glacial and hypsithermal times have had a great deal to do with their present floristics. For example, Simpson (1974) showed that the larger sizes of Andean páramos as they existed at full glacial are more highly and significantly correlated with numbers of plant species per páramo than are the present sizes of each páramo. Also, the distance between páramos at full glacial is almost statistically significant in regard to present-day floristic richness—but the effect of present distance between páramos upon floristic composition is not statistically significant.

Present-day alpine climates on the Great Basin mountains are quite cold during the winter. In this respect, basin alpine climates are probably comparable in winter temperature to alpine areas of the Rocky Mountains and the Sierra, although very few alpine weather data exist to substantiate this. In summer, the basin mountains are far cooler than the desert below. Daytime summer maximum air temperatures are lowest on crests and ridges and nighttime minima are lowest in cirques and canyons; the same relative conditions exist in the Rocky Mountains and Sierra Nevada.

These Great Basin alpine areas are considerably moister than the desert valleys in both winter and summer. However, except for the Ruby Mountains and nearby ranges, they are drier on an annual basis than alpine regions of the Rocky Mountains or the Sierra Nevada because they receive less snow. But they do receive enough snow to form persistent drifts in the lee of cliffs and ridges. It is such drifts that shorten the alpine growing season, keep plants well watered, and allow the growth of alpine plants of certain species. The ranges toward the southwestern part of the basin are relatively drier than the rest because they lie in the most extreme part of the Sierran precipi-

tation shadow. There is a trend toward more winter snow and summer rain in a traverse across the basin in an easterly direction toward the Rocky Mountains. The summer rains in the east are usually in the form of freshening thundershowers, which, I believe, have much to do with the survival so far south of populations of certain arctic species in the Rocky Mountains and eastern basin ranges.

These mountains were much colder and wetter during glacial times up to at least 12,000 years BP. Permanent snow was abundant, and many of the ranges had valley glaciers. These glaciated ranges include the White Mountains, Toiyabe, Santa Rosa, Independence, Jarbidge, East Humboldt, and Ruby Mountains. In the latter range, valley glaciers emerged from the mountains onto the now sagebrush-covered plains. Even far to the south, there were glaciers on the Spring Mountains² and San Francisco Peaks. Even though these glaciers were small as compared to glaciers and icefields on the Sierra and in the Rocky Mountains, they did create cirques which are now the refugia for a number of alpine species. The colder, wetter climate also depressed and telescoped vegetational zones and lowered timberlines an estimated 600 to 1200 m (Baker 1970, Loope 1969, Wells and Berger 1969). Even though timberline in itself is neither the only nor the best indicator of alpine conditions, such a depression would have greatly increased the size of basin range alpine islands and decreased the distances between them. This situation would have increased the chances of establishment of arctic-alpine species by long-distance dispersal and, in certain instances, by direct migration over tundralike terrain. Since timberline depression has been variously estimated and since it did undoubtedly vary from one part of the Basin to another, I have compromised by showing in Figure 1

²In botanical literature, the Spring Mountains are frequently, but incorrectly, called the "Charleston Mountains" due mainly to the title of Clokey's (1951) flora of the central portion of the range dominated by Charleston Peak.

what a 900 m depression would do to the sizes and proximity of alpine islands and continents at full glacial.

Not only have the alpine islands been larger in the past, they have also been smaller. During the hypsithermal, about 7500 to 4500 years BP, timberlines of *Pinus longaeva* in the White Mountains and the Snake Range advanced upward to a level about 100 to 150 m above where they now stand (LaMarche and Mooney 1967). Such a long period of warmth and aridity could have eradicated some alpine species by forest shading or by eliminating their snowy refugia on the higher peaks.

The hard rock geological history of the Basin Ranges is a complex and varied one. I shall not go into it here. Suffice to say that sedimentary rocks, and thus calcareous substrata, are more abundant in the eastern ranges while the western rocks tend to be igneous or metamorphic, and yet with some dolomites and other calcareous types. To many alpine plants, the chemical natures of these different kinds of substrates are all-important in marginal habitats.

ALPINE VEGETATIONS AND FLORAS

In any study of vegetation and flora, it is important to distinguish clearly between "origin" and "maintenance" of each. Origin is very difficult to pinpoint, and particularly so with alpine floras because they leave almost no macrofossils. However, the presence of diploids in widespread polyploid arctic-alpine species may play the role of "cytological fossils." The origin of a particular flora on any mountaintop is the result of the interaction of many factors: past geologic events, past climates, migrations of each species, polyploidy, evolution, and even man's activities. Hypotheses are numerous; answers are few.

While maintenance of an alpine flora and its vegetation is somewhat easier to understand, there is still much work involved. One must measure the characteristics of both the physical and biological aspects of

environment, preferably along meso- and microtopographic gradients throughout the year (Billings 1973). Also, it is necessary to know the tolerance ranges of plant populations in any particular place. This requires many field measurements and much laboratory experimentation under controlled conditions. We have made only a beginning in understanding maintenance of some alpine plant species. Such studies require the interaction of many people; they are not one-person jobs.

ALPINE VEGETATIONS

In trying to reach at least a partial understanding of alpine phytogeography and ecology in the Great Basin, it is helpful to start by describing alpine vegetations as they now exist from the Rocky Mountains across the basin ranges to the Sierra Nevada. A good approach is to look at these vegetations along a northeast to southwest transect from the Beartooth Mountains on the Montana-Wyoming line to the central Sierra Nevada. Such a transect crosses many of the basin ranges, but of particular interest are the Ruby Mountains, the Toiyabe Range, and the White Mountains. These represent the eastern, central, and western basin ranges, respectively.

Quantitative analyses of alpine vegetation have been made in the Beartooth Mountains (Johnson and Billings 1962), the northern Ruby Mountains (Loope 1969), the White Mountains (Mooney 1973), and the central Sierra Nevada (Chabot and Billings 1972). I do not know of any quantitative alpine vegetational data from the Toiyabe or Toquima Ranges; perhaps there are some. The floristic information and photographs in Linsdale et al. (1952) are of some help, as are personal qualitative observations which I made in 1949.

Space does not allow the presentation of those long tables of vegetational composition which do exist; one simply can refer to the publications listed above. However, the alpine vegetation of the Beartooth Moun-

tains is typically Rocky Mountain alpine with large expanses of alpine tundra in the true sense: *Geum rossii* turf in mesic sites, *Deschampsia caespitosa* meadow in moist sites, and *Carex scopulorum* in wet bogs. The crests and ridges are occupied by rather dense stands of cushion and rosette plants with *Silene acaulis*, *Carex elynoides*, and many other species dominating. Early and late snowbeds are abundant and have characteristic species surrounding them.

Alpine vegetation in the Ruby Mountains lacks the broad expanses of tundra characteristic of the Beartooth. However, south of Lake Peak along the divide there is fairly extensive tundra at elevations from 3140 m to 3300 m. This alpine vegetation is characterized by *Silene acaulis* and *Carex pulvinata*. Similar alpine vegetation exists at the same elevation on the north slope of Wines Peak, with *Geum rossii* and *Silene acaulis* being the dominants. *Carex scopulorum* grows in dense stands around alpine ponds. Some of the best-developed alpine vegetation in the Rubies is in the cirque floors. In Island Lake cirque, the vegetation is dominated mainly by *Erigeron peregrinus*, *Salix arctica*, *Caltha leptosepala*, *Geum rossii*, *Sibbaldia procumbens*, and *Polygonum bistortoides*. *Oxyria digyna* is common on rocky, moist sites, particularly around snowbanks. One is struck with the remarkable similarity in species composition and site characteristics to the alpine vegetation of the Beartooth some 700 km to the northeast. Essentially, the alpine vegetation of the Ruby Mountains is a small, only slightly attenuated, isolated example of Rocky Mountain alpine vegetation.

In strong contrast, the alpine vegetation of the Toiyabe Range, only 250 km southwest of the Rubies, apparently bears little resemblance to that of the northern Rubies or to that of the Rocky Mountains. It seems to be an open, rocky vegetation with a few scattered alpine grasses such as *Trisetum spicatum* and various species of *Draba* and *Eriogonum*, some of which are endemic. There is not the great variety of alpine veg-

etation types which one sees in the Rocky Mountains. More vegetational work is needed in the small and little-known alpine areas of the central Great Basin; further study may change our ideas of these regions of what might be termed alpine desert.

Another 150 km farther southwest is the long and high massif of the White Mountains. In contrast to the Toiyabe and Toquima Ranges, this has been rather intensively studied environmentally, vegetationally, and floristically. The alpine vegetation has been well-described by Mooney et al. (1962), Mitchell et al. (1966), and Mooney (1973). Over most of the extensive alpine area in the White Mountains, the vegetation is extremely sparse; Mooney (1973) reports a plant cover of only 1.5 percent at 4175 m on the side of White Mountain Peak. Mitchell et al. (1966) say that vegetational cover on windy, gravelly flats on Pellisier Flats, an area of 21 km² near the north end of the range, rarely exceeds 15 percent. However, on seepage banks and meltwater runs, vegetational cover ranges from 10 to 95 percent. Pellisier Flats at 4100 to 4430 m has active frost polygons and miniature solifluction steps reminiscent of the Beartooth Plateau. The most striking vegetational feature of the White Mountains, however, is the sharp distinction in vegetation and flora between the dolomite barrens and granite or quartzite fell-fields. The dolomite barrens are very desertlike and, although in places they may have vegetational cover up to 12 percent, in other places there are almost no plants. *Phlox covillei* and *Eriogonum gracilipes* are characteristic species on the dolomite. A granite fell-field at 3870 m had a vegetational cover of 50 percent and was dominated by *Trifolium monoense* and *Koeleria cristata*; the first is essentially endemic to the White Mountains and the second is a cosmopolitan species. The alpine vegetation of the White Mountains is decidedly unlike that of the Rubies—but both are Basin ranges.

There have been several vegetational studies made on alpine vegetation in the

Sierra Nevada. These vary considerably between the northern end of the range and the southern, where the peaks are higher and the climate drier. Only 48 km southwest of the White Mountain crest and within sight of it, is Piute Pass at 3540 m on the Sierran white granite. Here, Chabot and Billings (1972) found the low alpine vegetation covering less than 30 percent of the rocky ground and characterized by *Lupinus breuieri*, *Antennaria rosea*, and *Carex helleri*. Other common Sierran alpine species in similar locations on nearby peaks and ridges are *Phlox caespitosa*, *Penstemon davidsonii*, *Ivesia pygmaea*, and *Draba lemmonii*. At higher elevations, *Oxyria digyna*, *Polemonium eximium*, and *Hulsea algida* are constant members of the alpine vegetation usually on scree slopes. The most luxuriant vegetation near here is along snowbank meltwater brooks where *Dodecatheon jefreyi*, *Lewisia pygmaea*, and *Sedum rosea* occur. On very thin granitic soils which dry out after snowmelt, only *Calyptidium umbellatum*, the dwarf *Koenigia*-like endemic *Polygonum minimum*, and one or two other species can exist. There is a great difference in alpine vegetation here, not only from that of the Beartooth but also from that of the White Mountains on the near horizon.

ALPINE FLORAS

While there are a few floras for whole mountain ranges between the Rocky Mountains and the Sierra, e.g., Lloyd and Mitchell (1973) for the White Mountains, the main sources of alpine floras per se appear to be journal papers or theses. Referring again to Figure 1, I have assembled at least tentative figures on the numbers of alpine species for the same NE-SW transect along which the trend in alpine vegetation has been described. These figures will certainly be changed with additional collecting and publication, particularly of more volumes of Cronquist et al. Intermountain Flora and Howell's proposed Sierran Flora. The sources are the Beartooth Mountains (Johnson and Billings 1962), the Deep Creek

Mountains (McMillan 1948), the Ruby Mountains (Loope 1969), the Toiyabe Range (Linsdale et al. 1952), the White Mountains (Mitchell et al. 1966), and the central Sierra Nevada (Chabot and Billings 1972). Additionally, I have included floristic data from a series of three isolated alpine areas across the southern desert region. From west to east these are Olancha Peak and its neighbors in the Sierra Nevada (Howell 1951), the Spring Mountains (Clokey 1951), and San Francisco Peaks (Little 1941).

Many alpine plant species also occur in the Arctic. As a basis for whether or not our species do, I have checked each against Polunin's (1959) Circumpolar Arctic Flora. Species which are not arctic-alpine may be endemic to a continental region of the middle-latitudes or to the mountain range itself or its near neighbors. While we need much more information on both scores, the absolute figures on arctic and endemic species in each small alpine area can tell us something about migrations into an area and possibly about the evolution of new species after such migrations from afar or from the arid regions below. Nor should we forget that some endemic species may be relicts or that some widespread arctic-alpine species may have become extinct during-xerothermic times, or that some may never have reached certain alpine areas because of lack of adaptation for long-distance dispersal.

The upper part of Table 1 (the Beartooth-Sierra transect) illustrates immediately that there are many alpine species in the central Rocky Mountains that also occur in the Arctic. In the Beartooth Mountains, 91 out of 194, or almost half the alpine flora, also occurs in the Arctic. This is in contrast to the 24 arctic-alpine species in the Deep Creeks and 47 in the Rubies; but these are somewhat smaller ranges. The composition of the alpine floras of both of the latter ranges, however, is very much a Rocky Mountain-type flora. In contrast, west of the Ruby Mountains there is a dramatic drop in not only the total numbers of

alpine species in the Toiyabe, the White Mountains, and the Sierra Nevada, but also in the number of arctic-alpine taxa present. The arctic-alpine element consists, in these ranges, mostly of such easily dispersed, ubiquitous species as *Oxyria digyna*, *Trisetum spicatum*, *Cystopteris fragilis*, and *Androsace septentrionalis*. Even common species such as *Silene acaulis* are missing, not to mention relatively rare taxa such as *Koenigia islandica*, *Saxifraga flagellaris*, or *Phlippsia algida*. Widespread arctic-alpine species such as *Silene acaulis*, *Polygonum viviparum*, and *Salix arctica* reach their western limits in the Great Basin in the Ruby Mountains and do not reappear in the Sierra Nevada (Loope 1969). Since these species are not that particular in their environmental requirements (there are apparent places in the Sierra Nevada where they could grow), they either must be poorly adapted to long-distance dispersal or there is or has been an advantage to migrating north or south along the old tried and true Rocky Mountain pathway. Those arctic-alpine species in the Sierra Nevada most likely came down from the north in glacial or cooler times during the Pleistocene. Mi-

gration across the Great Basin appears to have been a chancy thing even at full-glacial. Only species with propagules easily dispersed by wind or birds appear to have made it to the central Great Basin mountains. Even after possible establishment, some alpine species may have become extinct on the Great Basin peaks in dryer, postglacial times. Axelrod (1976) also suggests extinctions of moist environment sub-alpine conifers and alpine species in the Great Basin during these xerothermic episodes. I believe that extended post-glacial dry periods also could have eliminated such dry-site arctic-alpine species as *Silene acaulis* and *Saxifraga cespitosa* in the Sierra Nevada where they do not occur today. This suggestion, of course, must assume that these species migrated into the Sierra Nevada, probably from the north, during favorable Pleistocene times.

Looking at the southern transect in Table 1, the same dearth of arctic species is apparent in the Olancha Peak group at the southern end of the Sierra and particularly so on Charleston Peak in the isolated Spring Mountains where only 9 arctic species are known to occur. In contrast, only

TABLE 1. Total numbers of true alpine species and those which also occur in the Arctic (arctic-alpine) in two transects across the Intermountain Region. Data from several sources.

Location	Total No. of Alpine Species	No. of Arctic-Alpine Species	Percent of Arctic-Alpine Species
NORTHERN TRANSECT			
Beartooth Mts.	194	91	47
Deep Creek Mts.	80	24	30
Ruby Mts.	189	47	25
Toiyabe Range	48	11	23
White Mts. (Pellisier Flats)	48	10	21
Piute Pass (Sierra)	41	4	10
SOUTHERN TRANSECT			
Olancha Pk., etc. (Sierra)	102	13	13
Spring Mts.	39	9	23
San Francisco Pks.	49	19	39

350 km to the southeast, the San Francisco Peaks have at least 19 arctic species in spite of their isolation. Also, there is a distinct Rocky Mountain cast to their alpine flora. A possible pathway for migration into this Pleistocene volcanic mountain may have been at full-glacial through the Arizona White Mountains to the southeast, or the source may have been through the Wasatch Plateau to the north. Again, we come to the origin versus maintenance problem: these arctic species would not remain in the volcanic cinders or the glacial cirques of this isolated mountain, no matter how they got there, except for the summer thunder-showers reinforcing the winter snows as a source of water.

Much more poorly known are the endemics of all of the above mountain ranges. Alpine endemics are much less common in the central Rocky Mountains than in the Sierra Nevada. This may be due to lack of isolation along the Rocky Mountain system. The Sierra Nevada as a whole has many endemic alpine species but I do not know how many of these may be narrow endemics restricted to the two small regions listed in Table 1. The White Mountains have several alpine endemics, and since they cover so much less area than the Sierra Nevada, the chances of these being narrow endemics are better than in the latter range. The same fact holds true for the isolated ranges of the central Great Basin. Some of these latter endemics may also prove not to be so narrow, except edaphically, upon further exploration. For example, consider *Primula nevadensis* (Holmgren 1967). The isolated Spring Mountains, with an alpine flora of only 39 species at most (some of these are probably subalpine), has at least 4 endemic alpine species. It seems that alpine endemism tends to be more common in relation to total alpine floras on isolated, nonvolcanic peaks and ranges in the southwestern part of the Intermountain Region; this includes the southern part of the Sierra Nevada. The real answer to the question of distribution of endemics lies in more collecting in alpine

environments and systematic description of the taxa.

One way of comparing alpine floras is to use Sørensen's (1948) Index of Floristic Similarity. This is expressed as:

$$IS_s = \frac{c}{1/2 (A + B)} \times 100$$

where, IS_s = Sørensen's Index of Similarity

c = number of species held in common by two alpine areas

A = total number of alpine species in Region A

B = total number of alpine species in Region B

Taking the available alpine floristic data from each of the nine alpine areas on both transects, I calculated Sørensen's Indices for each possible comparison. These indices are presented as percentage values in Table 2. Also, in the same table, direct distances in km between the alpine areas are shown. When the Indices of Similarity are plotted against distance for each pair of alpine areas, the result is a great deal of scatter in the points. There is little evidence of inverse correlation of floristic similarity between these alpine regions with distance. Out of 36 possible combinations, only 4 show indices above 30 percent combined with distances below 200 km. These are the Deep Creek—Ruby Mountains in the east-central Great Basin and Pellisier Flats—Olancho Peak, Pellisier Flats—Piute Pass, and Piute Pass—Olancho Peak, all in the Sierra Nevada—White Mountain complex at the extreme southwestern edge of the Great Basin. Two others had indices almost equally as high but at distances between 500 and 700 km; these are the Deep Creek Mountains—San Francisco Mountains and Beartooth—Ruby Mountains combinations. The most distant range, the Beartooth, has higher indices of similarity with the Ruby Mountains, Deep Creek Mountains, and San Francisco

Mountains alpine floras at distances of 650 to 1100 km than any of these latter ranges have with the Spring Mountains at distances less than 500 km. The distant Rocky Mountains alpine flora as exemplified by that of the Beartooth has as great or greater an influence on those of most of the Great Basin mountain ranges than does that of the much closer Sierra Nevada. There is even a greater (two to three times) similarity between the alpine floras of San Francisco Mountains and the Deep Creek Mountains at a distance of 531 km than there is between the Deep Creek flora and those of the Sierra Nevada and White Mountains, which

are equally distant from the Deep Creek Mountains.

The rather low indices of similarity indicate at least one fact rather clearly: these Intermountain Region alpine areas are very much like newly isolated islands. This is well illustrated along the southern transect from Olancha Peak to Charleston Peak to San Francisco Peaks. With the two gaps being only 225 and 378 km across, respectively, the indices of similarity are only 13 and 14 percent. The Olancha Peak group is clearly Sierran, Charleston Peak is unique, and San Francisco Peaks show strong relationships to the Rocky Mountains and

TABLE 2. Sørensen's indices of floristic similarity (in percent) between alpine floras for all combinations of alpine areas in both transects. Numbers in parentheses are distances (in km) between the alpine regions. Also, see map in Fig. 1.

Northern Transect						
	Bear- tooth	Deep Creeks	Ruby Mts.	Toiyabe Range	Pellisier Flats (White Mts.)	Piute Pass (Sierra)
Beartooth	—	24%	33%	14%	14%	9%
Deep Creeks	(676)	—	39%	22%	19%	10%
Ruby Mts.	(692)	(153)	—	20%	14%	11%
Toiyabe Range	(917)	(322)	(257)	—	21%	16%
Pellisier Flats (White Mts.)	(1102)	(451)	(418)	(145)	—	34%
Piute Pass (Sierra)	(1167)	(515)	(483)	(217)	(72)	—
Olancha Pk. Group (Sierra)	(1223)	(547)	(539)	(290)	(169)	(129)
Spring Mts.	(1110)	(434)	(475)	(325)	(298)	(306)
San Francisco Pks.	(1086)	(531)	(668)	(636)	(660)	(668)
Southern Transect						
	Olancha Pk. Group (Sierra)		Spring Mts.		San Francisco Pks.	
Beartooth	14%		8%		23%	
Deep Creeks	15%		13%		31%	
Ruby Mts.	14%		8%		19%	
Toiyabe Range	13%		18%		21%	
Pellisier Flats (White Mts.)	36%		16%		19%	
Piute Pass (Sierra)	32%		10%		4%	
Olancha Pk. Group (Sierra)	—		13%		13%	
Spring Mts.	(225)		—		14%	
San Francisco Pks.	(603)		(378)		—	

mountain ranges far to the north. These affinities of the San Francisco Peaks alpine flora have also been noted by Moore (1965).

After examining the existing floristic data on alpine species across the Great Basin, it is tempting to delineate some alpine phytogeographic boundaries. Certainly, there is a sharp boundary just west of the Ruby Mountains separating Rocky Mountain types of vegetation and flora from that of the Great Basin. Where this boundary goes to the south, I am not prepared to say. Certainly, it would appear to be west of the Snake Range and perhaps west of the Grant Range; but this is tentative and probably premature. It obviously lies between San Francisco Peaks and the Spring Mountains.

Another alpine phytogeographic boundary lies between the White Mountains and the Sierra Nevada and winds north in sinuous curves until it divides the Carson Range on the west from the Pine Nut Range on the east; but several species pay no attention to such an imaginary line and go their way from the Sierra Nevada into the altered andesites of the Virginia Range (Billings 1950) and the nevé cirques of the Pine Nut and Wassuk Ranges (Billings 1954). Again, if edaphic or moisture conditions are right, some species can get to seemingly inhospitable mountain ranges and stay there perhaps by infraspecific physiological adaptations (i.e., ecotypes).

POSSIBLE ORIGINS OF INTERMOUNTAIN ALPINE FLORAS

Alpine floras originate in all mountains by migration and/or evolution; the mountains of the Intermountain Region are no exception. Refugia, both glacial and interglacial, are also important. As Figure 1 shows, and as Simpson (1974) has demonstrated for the páramos, successful long-distance dispersal is greatly influenced by the sizes and proximity of alpine islands. Such islands were obviously larger and closer during glacial and cooler times. From distributional evidence, only a relatively few

arctic-alpine species appear to be able to migrate far: *Oxyria digyna*, *Saxifraga cespitosa*, *Trisetum spicatum*, and *Cystopteris fragilis*, for example. Therefore, it is advantageous for ancestral species to be nearby when mountains arise or new alpine areas come into existence by climatic causes. It also seems to be advantageous to be on a north-south migration route such as the old Rocky Mountains, or even the much younger Cascade-Sierran system. The ability to evolve rapidly by adaptive radiation is also advantageous, as for example, in the genus *Espeletia* in the Andean páramos.

Such plasticity, plus pure luck in being near refugia, either edaphic or microclimatic, also helps. Interglacial refugia are fully as important as glacial refugia. Such interglacial refugia can be mountaintops such as Mount Washington, New Hampshire, altered volcanic rocks as in the Virginia Range of western Nevada (Billings 1950), alpine snowbanks, and the moist, cool floors of impervious cirques (Loope 1969). Loope ascribes the presence of many arctic species in the Ruby Mountains today to its nonporous (moist) cirque floors as compared to the porous, dry cirque floors of the Jarbidge Mountains to the north and those of the Snake and Schell Creek ranges to the south.

There are other sources of alpine floras in the Intermountain Region. These are the surrounding desert floras as suggested long ago by Went (1948) and experimentally investigated by Klikoff (1966) and by Chabot and Billings (1972) for the Sierra Nevada. The principal findings reported in the latter paper would apply almost as well to the mountain ranges of the Great Basin, provided there are suitable sites for such migration and evolution, and providing there are species and genera of sufficient genetic plasticity near at hand. The derivation of a new alpine flora from a desert or semidesert flora is aided by the following:

- a. preadaptation of winter annuals and perennials in regard to physiology and morphology,

- b. the ability to migrate upward during favorable climatic periods into new but not altogether dissimilar environments,
- c. selection for metabolism at low summer temperatures,
- d. selection for low temperature starch degradation and sugar translocation at night,
- e. selection of populations and ecotypes which acclimate metabolically rapidly and ideally, and
- f. selection for flowering and seed-set in short, dry cool growing seasons.

These have been elaborated in detail by Billings (1974).

There is every reason to believe that such upward evolution of new "alpine-desert" taxa is taking place in the Great Basin. But the rate may be slower than in the Sierra Nevada due to a smaller preadapted flora and also due to the drier and less snow-protected environments on the peaks. In such a case, there could be a trend toward edaphic endemism because other kinds of habitat diversity are in relatively short supply. Such upward mobility and long-distance dispersal over great distances in a north-south direction seem to be the principal sources of the alpine floras of these isolated montane islands in the central Great Basin.

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PHYTOGEOGRAPHICAL VARIATION WITHIN JUNIPER-PINYON WOODLANDS OF THE GREAT BASIN

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ABSTRACT.—About 22 percent of the pigmy conifer woodlands of the United States occur within the Great Basin. Only a very few reports of these woodlands exist in the literature. Available reports are either of general descriptive nature or specific analysis of vegetation-environmental relationships on one mountain range. In order to better understand basin-wide synecological patterns, a cooperative study was carried out by personnel at Utah State University and the University of Nevada-Reno between 1972 and 1975. Vegetation, landform, geology, and soils data obtained from 463 systematically placed stands on a randomly chosen set of 66 mountain ranges have been used to derive patterns of latitudinal, longitudinal, and altitudinal variation in the floristic diversity in juniper-pinyon dominated woodlands across the Great Basin.

The latitudinal-longitudinal patterns show greatest environmental and floristic diversity on the higher mountain ranges on the southern end of the Central Plateau portion of the study area where the Great Basin-Mojave Desert transition occurs. This is also where the elevational breadth of the woodland belt is greatest. Juniper-pinyon woodlands are largely lacking from northwestern Nevada. The lowest elevations for the type are found in the Dixie Corridor centered in southwestern Utah. The general elevation of these woodlands is highest in the west-central part of the Great Basin and declines both toward the Sierra Nevada on the west and the Wasatch Front-High Plateaus on the east.

Use of the equilibrium theory of island biogeography gave incomplete explanations of the diversity patterns observed. Certain conceptual and methodical problems forced by this overly simplistic theory are discussed. The best correlations obtained were between species richness and an index of ecotopic diversity.

Correlation of Basin-wide patterns of woodland floristics with surficial geology, landforms, and soils is non-discriminatory. However, broad-scale, phytogeographical variations in these woodlands are closely associated with climatic differences. Although much direct climatic data are lacking, it seems likely that the relative contributions of the transitory frontal systems moving inland from the Pacific, continental cyclones developing over the Great Basin, and convective storms associated with the moist air from the Gulf of Mexico to induce precipitation at different seasons are regionally important in the causation of vegetation distribution and composition.

The instability of temperature inversions is a likely determinant of the position of woodlands along the northern boundary of the type. The Pacific frontal systems break the inversions most readily and are thought to be the major cause for the lack of this vegetation in northwestern Nevada and on exposed mountain ranges along the northern boundary of the type. Such observations provide leads for relevant ecophysiological research to support or reject these notions.

The juniper-pinyon woodlands are a major vegetation type of the Intermountain West. West, Rea, and Tausch (1975) have indicated that about 325,000 km² (125,000 mi²) are involved. About 7.1 million ha, or 22 percent of this total, occur in the Great Basin. It is the phytogeography of this portion of the type that we wish to consider here.

Brief descriptions of the Great Basin pinyon-juniper woodlands, along with con-

siderations of other Great Basin vegetation types and their distributions have been made by Billings (1951), Cronquist et al. (1972), Tueller (1975), and Young, Evans, and Tueller (1976). They all characterized these woodlands as generally covering low hills or as forming a belt of vegetation at lower elevations on the higher mountains with sagebrush-dominated belts both above and below.

Beeson (1974) mapped the typed and de-

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scribed the general longitudinal and latitudinal variations from a large set of vegetational data collected on approximately one-third of the mountain ranges found in the Great Basin. In this paper we wish to examine further aspects of this and additional data, expanding the discussion of longitudinal, latitudinal, and elevational floristic diversity (beta diversity, according to Whittaker 1975) and propose possible explanations for some peculiarities of latitudinal limits and variations in elevational extent of the type.

METHODS

Data set collection and prior analysis:

The data set available involves quantitative data on landform, geology, soils, and vegetation collected between 1972 and 1975 for 463 stands systematically placed on a randomly chosen set of 66 Great Basin mountain ranges (Nabi 1978).

We defined woodlands as having at least 25 pinyon and/or juniper trees per hectare (10/acre). At least one tree had to be in our mature size-age-form class. These criteria kept the samples from extending too far into ecotones, yet allowed a good coverage of the main juniper-pinyon woodland type.

Stands were sampled at regular elevational intervals on all of the four major exposures where the juniper-pinyon belt existed on each mountain range. We are therefore able to discuss the Basin-wide distribution of these woodlands from fairly objective bases. The full details of the sampling design, data collection, and prior analysis are given elsewhere (Nabi 1978).

Supplementary sampling of the Shoshone Mountains added stands in broad canyon bottoms and on secondary slopes of faces along major ridges. These additions were made to sample for one area a greater range of ecotopic heterogeneity than was provided by the regularly placed upland sites on exposures in cardinal directions.

In addition to presentation of broad, longitudinal-latitudinal patterns of woodland

distribution via a map derived from field-checked space photography, Beeson (1974) grouped the sampled mountain ranges into three first-order divisions, based on floristic composition. The stress was on the major species found on at least 25 percent of the mountain ranges sampled. These major species were commonly found in most of the stands on the mountain range where they occurred.

This approach yielded one group of ranges with moderate floristic diversity in the Central Plateau region that had considerable similarities to the foothills and ranges directly adjacent to the Sierra Nevada on the west and the Wasatch Front-High Plateaus of central Utah on the eastern boundary of the basin. Another grouping with low floristic richness was designated for all lower elevation ranges occurring in the generally lower, drier portions of the Great Basin. The third grouping consisted of ranges with the highest floristic diversity. These all occurred along the southern end of the Central Plateau where the Great Basin-Mojave desert transition occurs.

These floristic units were related to patterns of surficial geology, landform, soils, and climate. Weak correspondences were found at this scale with all environmental factors except climate. The widescale longitudinal-latitudinal differences observed were therefore thought to be largely related to current patterns of precipitation and temperature.

Current analysis methods: Mueller-Dombois and Ellenberg (1974), in their recent textbook on the *Aims and Methods of Vegetation Ecology*, emphasize that a complete understanding of the distribution of plant communities involves a consideration of flora, accessibility, ecological properties of the plants, habitat, and time. Our further analysis here involves an in-depth examination of the total floristic diversity in our samples of Great Basin pigmy conifer woodlands in an attempt to relate these floristic diversity patterns to likely paleocological influences and to present environmental

heterogeneity with emphasis on the present climatic patterns through space and time.

We also examined the appropriateness of applications of island biogeographical theory (Simberhoff 1974). These analyses followed a strategy similar to that used by Brown (1971) and Johnson (1975). Data from the 18 mountain ranges sampled at 200 m elevation intervals were used (Nabi 1978). The variables accounted for were total woodland species per mountain range, total mountain area, total mountain area occupied by woodland (taken from our previously published map), mountain height, width of barrier, and an index of ecotopic diversity.

The width of the barrier was calculated similarly to Johnson's (1975) approach except that we considered distance to the nearest of three "continental" areas: The Sierra Nevada, Wasatch Front-High Plateaus of central Utah, and the northern boundary of the Snake River Plains, all defined as in Cronquist et al. (1972).

The ecotopic diversity where woodlands occurred on each mountain was indexed by

the use of an arbitrary, numerical scale (Table 1) taking into account those variables on which we had direct data. The higher the variety of factor conditions, the greater the presumable ecotopic diversity. Untransformed data for the variables assessed are presented in Table 2. Correlation coefficients (r) between the variables were then calculated for both the raw and logarithmically transformed data.

Additional tabular and graphical organizations of the data were employed in order to clarify our broad-scale phytogeographical view of latitudinal, longitudinal, and altitudinal variation in these woodlands. A series of range-by-range comparisons were made on the basis of total species richness for each range, average stand species richness, and altitudinal distribution of the woodland. Each type of analysis was mapped and compared with each other and the broad-scale climatic patterns for the region.

RESULTS AND DISCUSSION

Overall species richness: A total of 367 vascular plant species were found within

TABLE 1. Point system for ecotopic diversity score.

		Range of Values Possible	Range of Values Observed
Exposure	Cardinal slopes having woodlands 1 = north only 2 = north and east, etc.	1-4	2-4
Slope	Number of slope classes (10% increments) 0-10% = 1, 0-10% plus 11-20% = 2, etc.	1-5	2-5
Elevation	Elevations at which woodlands were sampled (200 m intervals) 1800-2000 m = 1; 1800-2000 m plus 2001-2200 m = 2, etc.	1-4	2-4
Landform	Five major landforms encountered (valley, foothill, bajada, terrace, mountain) (defined in Nabi 1978)	1-5	1-5
Geology	classified to clan (Nabi 1978)	1-19	1-8
Soils	Classified to subgroup according to Soil Survey Staff, USDA, Soil Conservation Service (1951, 1960, 1967)	1-24	1-16
Total possible score		61	(10-40)

the juniper-pinyon woodlands sampled. The number of species in the woodlands on individual mountain ranges varied from 164 species on the Shoshone Mountains of west-central Nevada to under 30 species on small isolated ranges of western Utah. Figure 1 shows that most of the mountain ranges had fewer than 50 species in their woodlands. Furthermore, the ranking of species numbers per mountain range frequencies (Fig. 2) shows an expected log-normal distribution over the sampled ranges (May 1975). Many species were found at only one stand on a given mountain range. If the species frequency sequence is plotted against the number of stands in which they occur (Fig. 3) the right hand portion of the curve also follows a log-normal form. The frequency values for the rare species (those occurring in one to four stands) are in excess of the expected value (Fig. 4). These high frequencies of rarer species are indicative of an over-saturation of relictual species probably remaining from the vegetation migrations resulting from the more favorable climate of the recent geologic past. This is a situation similar to that found by Brown (1971)

for small mammals and Johnson (1975) for permanent resident birds in the same area. Our estimates of such oversaturation are conservative since sampling was restricted to upland areas on all ranges except the Shoshone Mountains, which included some broad drainage bottoms and major ridge faces. Judging from the high species density of the Shoshone Range, inclusion of more pronounced topographic situations such as narrow drainage channels and searches of atypical geological outcrops and unusual landforms on the other ranges, in addition to our predetermined sampling scheme, would have yielded more plant taxa within the woodland belt.

If the average number of species per stand within a given mountain range is plotted against the total number of species found in the woodlands of that range (Fig. 5) the envelope including the data points illustrates that there is a very general increase in stand diversity with increasing floristic diversity of the ranges sampled. The variation, however, is high. Except for the ranges with greatest and least diversity, there are few mountain ranges fitting with-

TABLE 2. Untransformed data used to test appropriateness of equilibrium theory of island biogeography.

Mountain Range	Pigmy Conifer Woodland Species Encountered	Total Area of Mountain' (km ²)	Total Area of Woodland (km ²)	Mountain Height (m)	Width of Smallest Barrier (km)	Ecotopic Diversity Score (See Table 1)
Burbank Hills	19	43	43	2384	36	10
Confusion	32	145	145	2461	39	13
Pine Valley	37	143	143	1989	10	18
Black Pine	38	458	113	2853	30	16
Toana	38	286	263	2117	31	19
White	40	1691	1305	3091	10	19
Goose Creek	42	1691	1305	2295	28	14
Tushar	46	1412	706	3713	10	18
Pilot	48	321	293	3265	20	24
Excelsior	48	187	187	2532	10	13
East Humboldt	49	592	54	2456	42	18
Schell Creek	54	1523	1076	3353	12	22
Mineral	65	298	187	2921	10	20
Monitor	69	1908	1564	2845	35	22
Toiyabe	76	2069	974	3292	42	24
Needle	93	1213	1083	2699	10	40
Highland	94	286	263	2865	15	27
Shoshone	164	519	450	3145	42	32
Mean	58.4	821.4	564.1	2793.1	24.0	20.5
S.D.	33.2	708.9	512.1	466.0	13.2	7.3

'Area above 1800 m.

in a similar range of limited average stand diversity. The majority of the mountain ranges within any total diversity class have a wide variation of average stand diversity. For example, in the interval of 80 to 95 species on a range, the average stand diversity varies from 9 to over 25 species.

Latitudinal and longitudinal diversity patterns: A currently fashionable way of explaining geographical patterns of diversity would be by application of island biogeography theory. The results of the correlations of total species richness with total mountain area, total area of woodland on the mountain, width of barrier, mountain

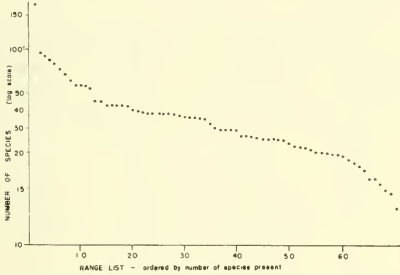


Fig. 1. Total number of plant species in the woodland belts on each mountain range ordered from the richest to the most depauperate.

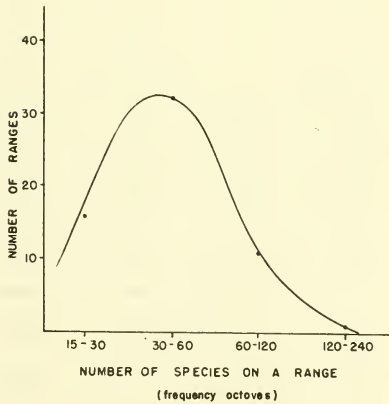


Fig. 2. Range frequency of total number of plant species in the woodland belts organized by frequency octaves. Line represents log-normal interpolation.

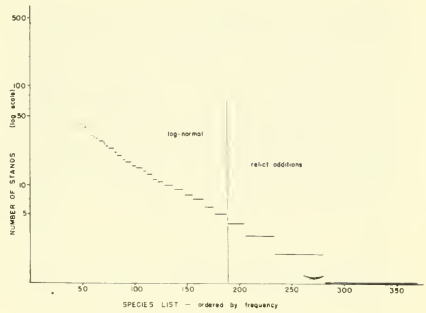


Fig. 3. Relationships of stand frequency to species richness. (366 stands of woodland on 66 mountain ranges.)

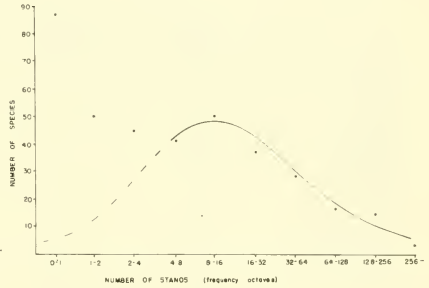


Fig. 4. Number of species ordered by number of stands in which they occurred (frequency octaves). Line represents log-normal interpolation.

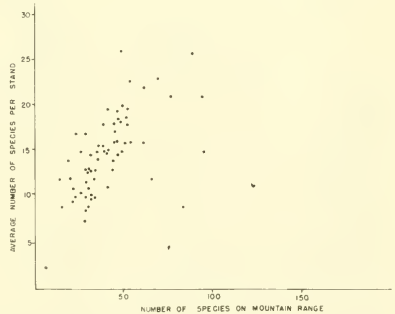


Fig. 5. Relationship of average number of species per stand with total number of species in the woodlands sampled on each of 66 mountain ranges.

height, and an ecotopic diversity score for each mountain range are given in Table 3.

The linear correlations of woodland floristic diversity with total mountain area, woodland area on the mountain, width of barrier, and height of mountain range are all low and not related in a statistically significant sense. There is, however, a significant relationship of the index of ecotopic diversity with floristic richness.

On a log-log basis the picture changes considerably. The correlation between ecotopic diversity and species density is highly

significant with little change in value, with or without data from the Shoshone Mountains. Species density is significantly correlated with total area and woodland area at the 0.05 level without the Shoshone Mountains and barely insignificant with them included.

The relationships between other factors shows scattered significance. Ecotopic diversity is significantly correlated with total mountain area and woodland area for both analyses. Mountain height and total mountain area, but not woodland area, are signifi-

TABLE 3. Correlation coefficients (r) between variables. Lower triangular matrix for log-transformed data, upper for untransformed data.

With Shoshone Mountains						
	Species Density	Ecotopic Diversity	Mountain Height (m)	Total Mountain Area (km ²)	Woodland Area (km ²)	Width of Barrier (km ²)
Species Density	—	.7846**	.3470	.1182	.1669	.1392
Ecotopic Diversity	.8570**	—	.3446	.2349	.3133	-.1355
Mountain Height	.4408	.4227	—	.4676	.3390	-.1743
Total Moun- tain Area	.4545	.4862*	.5326°	—	.9265**	.0068
Woodland Area	.4572	.5049*	.4620	.8510**	—	-.1108
Width of Barrier	-.3806	-.1691	-.1688	-.0743	-.2325	—
Without Shoshone Mountains						
	Species Density	Ecotopic Diversity	Mountain Height (m)	Total Mountain Area (km ²)	Woodland Area (km ²)	Width of Barrier (km ²)
Species Density	—	.8424**	.3303	.3354	.3479	-.2279
Ecotopic Diversity	.8521**	—	.2993	.3035	.3658	-.3125
Mountain Height	.4120	.3849	—	.4995°	.3565	-.2580
Total Moun- tain Area	.5612°	.5219°	.5422°	—	.9272**	.0459
Woodland Area	.5229°	.5198°	.4596	.8524**	—	-.0978
Width of Barrier	-.2763	-.3135	-.2413	-.0790	-.2629	—

* = $p \leq 0.05$ = ≥ 0.4820

** = $p \leq 0.01$ = ≥ 0.6060

icantly correlated. Total mountain area and woodland area are significantly correlated; however, all these variables are so inter-related that significant correlations are to be automatically expected. The discrepancy between the actual and perfect correlation is probably due to historical accidents such as fire eliminating some woodland from where it has potential on those portions of mountains where climatic unfavorableness exists, as will be explained later.

We interpret this failure of width of barrier to account for any of the variation observed to be at least partially due to a variety of methodical problems created by some simplistic decisions forced by the current development of the theory. First of all, it is impossible to choose one continent contributing flora to the woodlands. Any one mountain range has floristic affinities with all surrounding areas. The mixture could be better described by the degree of affinities to all possible continents. The Mojave desert also contributes to the understory composition. However, because some of the mountain ranges are imbedded in the Mojave Desert, we knew of no way to calculate barrier width in such circumstances.

The overall height of the mountain range probably yields a poor correlation because these woodlands have both boreal-derived and lowland-derived components. Thus, height of connecting ridges or valleys would have a variable effect on what species could have migrated across the Great Basin and have had a route of escape as environments changed. As Johnson and Raven (1970) have previously pointed out, height has inevitable covariation with total environmental diversity. Therefore, it is not surprising that the index of ecotopic diversity, which reflects combined physical variables, gives a much better correlation coefficient.

The linear relationship of the index of ecotopic diversity with species richness changes if the Shoshone Mountains, with their expanded sampling scheme, are excluded ($R^2 = .6156$ to $R^2 = .7096$). As can be seen from Figure 6, the increased sam-

pling on the Shoshone Mountains did not result in an obvious increase in ecotopic diversity, but it did give an obvious increase in the number of species encountered. This is possibly due to an increased microclimatic heterogeneity resulting from the sampling scheme used. Some minor changes also occurred for other relationships when Shoshone Mountain data was excluded (Table 3).

The influence of the increased sampling scheme on the results with the Shoshone Mountains has been minor with less effect on the log-transformed data than on the linear data. What this appears to show is that, within a reasonably uniform sampling scheme, the floristic diversity encountered within the woodlands is closely related to physical site diversity. This seems to be as much a function of where the plants can survive as it is a function of how many habitats exist on a particular range.

The primary contributor to the ecotopic diversity index is the number of different

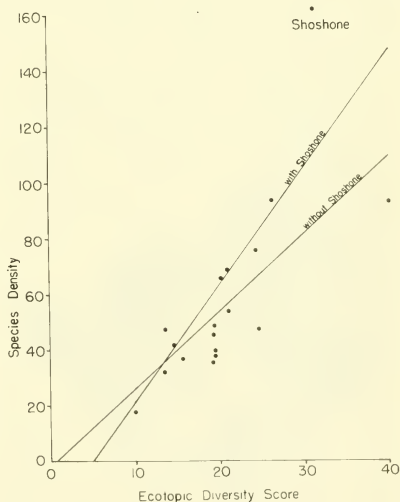


Fig. 6. Regression between ecotopic diversity index and species density in juniper-pinyon woodlands on 17 and 18 mountain ranges in the Great Basin (with and without the Shoshone Mountains included).

soil types encountered (Table 2). Analyses thus far completed have shown no relationship between any specific soil type and any specific vegetation composition on a Basin-wide basis. The diversity of soil and topographic conditions appears to indicate the potential for diversity of vegetation composition but not necessarily which taxa may be involved. This further complicates any attempt at an island biogeographical approach.

Attempts to map latitudinal and longitudinal differences in the equitability components of diversity were found to be of little value since juniper-pinyon woodlands are almost uniformly dominated by one or two trees plus one or two shrubs. One stand had only three species altogether. Most stands had only trace amounts of plants other than the most common five or six species. What equitability gradients that occurred are mostly elevational and successional, as will be demonstrated later. The species presence-absence approach is deemed more useful at the scale being focused on here (Hume and Day 1974, Schnell, Risser, and Hilsel 1976).

Floristic diversity (Fig. 7) is greatest on the higher ranges across the southern end of the Central Plateau portion of the study area where the Great Basin-Mojave Desert transition occurs. In addition to the relationship to the greater present environmental variation (Table 3), we feel that the high diversity there is partially due to historical probabilities of mixing of species with varying abilities of range expansion and survival in the considerable migration of species which has apparently taken place in and since the Pleistocene, particularly hypsithermal time (Antevs 1948 and 1955; Morrison 1965; Birkeland 1969; Spaulding 1974; Martin 1963; Martin and Mehringer 1965; Fritts 1965; Cottam, Tucker, and Drobnick 1959; LaMarche 1974; Phillips and Van Devender 1974; Van Devender 1974; Wells and Jorgenson 1964; Wells and Berger 1967; Elston 1976).

These previous papers and analysis of our

data favor the view that the pigmy conifer woodlands were once continuous across the Great Basin and northern Mojave Desert regions. Subsequent aridity and consequent plant migrations have fragmented these woodlands into the patterns of distribution seen today. The differences in floristic richness are probably more related to rates of extinction (Stebbins 1974 and 1975) than to long-distance dispersal from source biotas on the several possible continents. The richness of the present woodland flora is thus understandably related to the overall environmental favorability of the various mountain ranges at present and in the recent past.

Elevational variability: Billings (1951) and Hollermann (1973a and b) have previously commented on the puzzling variation in the elevational extent of Great Basin juniper-pinyon woodlands. We also noted wide variation in the Basin-wide elevational limits of this vegetation type. This variation, however, shows a close relationship to the general topography of the area, with climatic modification being important in the northern portions.

Our lowest sample in the juniper-pinyon

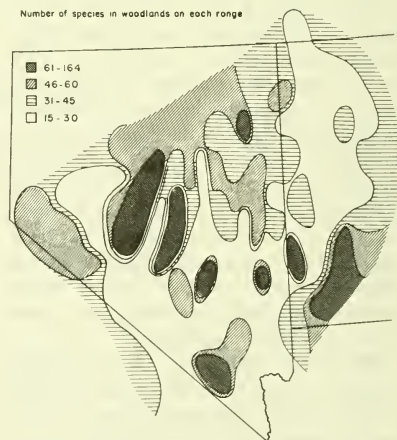


Fig. 7. Isolines of species richness in the woodlands between the 66 mountain ranges.

woodland was a stand at 1200 m on the south slope of the Beaver Dam Mountains of extreme southwestern Utah. This area is also the topographic low point of the area studied. The highest lower boundaries are found in the White, Excelsior, and Silver Peak ranges in the southwestern portion of the study area, and the Toquima and Monitor ranges of the central plateau, some of the highest parts of the topography of the whole study area. The regional distribution of the lowest woodland boundaries are definitely along the eastern and southern boundaries of the study area (Fig. 8).

The highest boundary of the woodland belt is much less definite (Fig. 9), largely due to great differences in mountain heights. The upper extreme of these woodlands in our data set was a 2800 m elevation stand on the west slope of the White Mountains of California. The geographical distribution of upper boundaries is partially correlated to those of lower boundaries.

The difference between the actual elevation of the lower limit and upper limit varies greatly from aspect to aspect on a mountain range and from range to range

over the Great Basin. An average woodland belt width of about 350 m elevational extent occurred on the mountain ranges we sampled. Further analysis of the data shows extremes of belt width ranging from over 700 m in elevation in the White Mountains of California, Highland Peak of Nevada, and the Needle Range of Utah to essentially zero at the northern boundaries of the type. The band of woodland is also extremely narrow in western Utah.

These elevational extremes and band widths are graphically portrayed in Figures 10 through 13, which depict transects across the Great Basin. These transects could be combined to make a response envelope. The breadth of these woodlands is generally greatest in the areas where the extremes of elevational extent occur. (Exceptions to this will be explained later). This greater breadth also approximately coincides with and contributes to the higher floristic diversity in the Great Basin-Mojave transition discussed earlier.

Although undoubtedly some of the elevational variation observed is due to recent historical causes, especially fire and wood

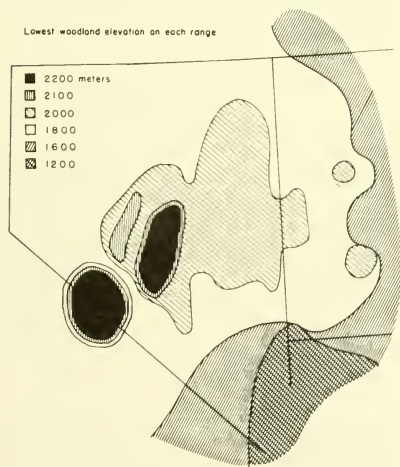


Fig. 8. Isolines of lowest woodland elevation sampled. Interpolation between 66 mountain ranges.

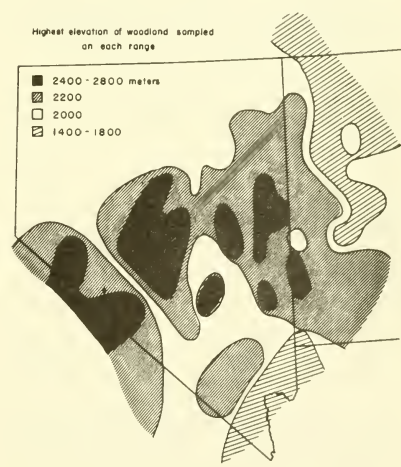


Fig. 9. Isolines of highest woodland elevation sampled.

cutting (Lanner 1976), there are consistent patterns of elevational extent related to topography and climate. The west and east relationships show this most clearly. Woodlands in the eastern Great Basin are generally lower than those to the west. The woodland belt also narrows considerably at the Wasatch Front. The average elevation increases, and then decreases, while the

width of the woodland type generally decreases from south to north.

The relative composition of the dominant trees and associated understory varies considerably within the belt (Fig. 11-13). The usual case is for pinyon to increase with altitude and juniper to dominate the lower half of the belt. On many of the higher mountain ranges in the Great Basin, the up-

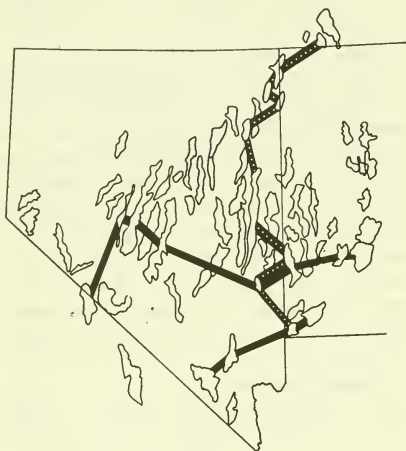


Fig. 10. Map of the mountain ranges sampled in this study. Lines connect the mountain ranges depicted in the following figures.

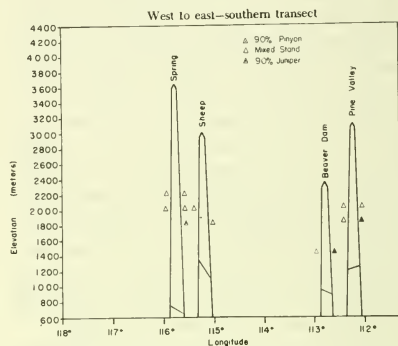


Fig. 12. Schematic cross section of the altitudinal and latitudinal variations in the woodland belt and its tree species dominants for a west-east transect (see Figure 10) of some of the southernmost ranges sampled. Lines across mountains indicate elevations of adjacent valley floors.

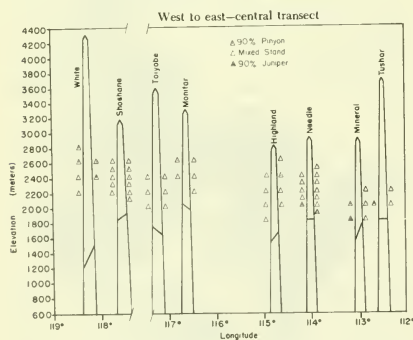


Fig. 11. Schematic cross section of the altitudinal and latitudinal variations in the woodland belt and its tree species dominance for a west-east transect (see Figure 10) of some of the southcentral ranges sampled. Lines across mountains indicate elevations of adjacent valley floors.

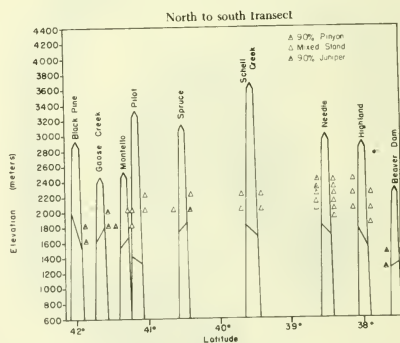


Fig. 13. Schematic cross section of the altitudinal and longitudinal variations in the woodland belt and its tree species dominants for a north-south transect (see Figure 10) in the Great Basin. Lines across mountains indicate elevations of adjacent valley floors.

per part of the woodland belt is a pure pinyon overstory. Juniper is more widespread, dominating areas in the north and at lower elevations that do not have pinyon. The quantity of juniper appears to increase with increasing soil moisture stress over most of the Great Basin.

The greater proportions of pinyon don't always appear to be purely due to increasing precipitation, usual at higher altitudes. Single leaf pinyon appears to have a wider range of moisture tolerance than does juniper at the higher moisture levels. The incidence of pinyon pine with double needles and amounts of juniper increases as the proportion of summer rainfall increases from west to east across the Great Basin. The summer dry, extreme western boundary of the basin is the only place where some mountain ranges have single-leaf pinyon but lack juniper. On the west side of the White Mountains there are belts of pure pinyon both above and below juniper (St. Andre, Mooney, and Wright 1965). These two circumstances suggest that although summer soil moisture stress may largely explain the lower elevational limits over most of the basin, the circumstances in the southwestern portion of the study area indicate that there may be temperature regimes unsatisfactory for juniper-pinyon mixes there.

St. Andre, et al. (1965) have speculated that lack of competition from extensive forest vegetation above the pinyon-juniper belt may explain the extreme width and high upper limit of the type on the White Mountains. The general absence of pinyon and juniper on the east flank of the Sierra might be partially due to Ponderosa pine and montane chaparral providing more competition than the sagebrush-grass types typical of the Great Basin Ranges. Similarly, oakbrush-dominated vegetation in the Wasatch Mountains and those near the eastern boundary of the Great Basin commonly occur above or replace juniper-pinyon woodland vegetation. Could oakbrush provide competition limiting the extent of the

pigmy conifer woodlands there? Could the likely upward migrations of juniper-pinyon woodlands and the other conifer belts (LaMarche and Mooney 1972) during the hypsithermal have resulted in the elimination of conifer forests at higher elevations of the smaller mountain ranges of the Great Basin? When temperature cooled and precipitation increased in more recent times (LaMarche 1974), pinyon and juniper could have expanded with less competition from other tree forms. Are current precipitation-temperature relationships suitable for more competitive species? Unfortunately, little direct data exists to answer these questions.

Ponderosa pine exists in a few scattered locations on the ranges of southwestern Utah and southeastern Nevada without dominance occurring. In those areas ponderosa pine seems to be limited to the most favorable sites, e.g., moist sites along streams or northeastern slopes. Pinyon and juniper compete largely with shrubs at both their upper and lower boundaries within the Great Basin.

Until more definitive evidence is in from palynological, dendroclimatological, and woodrat midden studies, we can only go on inferences from current vegetation. Although competitive and historical factors are part of the environmental complex, we feel that we can largely explain the current distribution of juniper-pinyon woodlands on the basis of recent and current climatic patterns.

The effect of mountain height and mass on climatic patterns (the "Merriam Effect," Lowe 1964) has long been recognized by plant geographers. Since its manifestations are greatest in semiarid regions, we related our data on width of woodland bands against the variables of maximum mountain height and area of the mountain mass. Narrower belts are generally found on the mountains of smaller area with the narrowest of the belts generally, but not always, found on those ranges with less than 700 km² area (Fig. 14). Mountain area above this size has little relation to the width of

belts. The widest belts are found on the highest peaks and are relatively independent of mountain area (Fig. 15). A high peak will not, however, necessarily have a wide belt of woodland (e.g., Wheeler Peak, Ruby Mountains, etc.). In circumstances where the belt is wide, the height of the peak dominates, but the location of the peak in the Great Basin is of much more importance. Figure 16 makes a separation of the Great Basin on the basis of where woodland belt widths are either greater or less than 400 meters. There are many peaks in the area of narrow belt width that are as high or higher than those found in the area of the wide belt width, but they are all in the region of greater orographic impact from Pacific Frontal storm systems (Houghton 1969). Because of their elevation, the very high ranges of east central Nevada have a climate similar to the ranges more north and west. These climatic controls will now be expanded on.

The lower woodland boundaries in the northern half of the study area appear to be related to valley bottom topography (Figs. 10-13). Wernstedt (1960) shows that little difference occurs in summer temperatures between the southern and northern Great Basin, but greatly lowered winter values are encountered as latitude increases. This trend applies best to valley bottom stations. Knowledge of temperature within the woodlands is minimal because few meteorological stations with long-term records exist. Most of the U.S. Weather Service meteorological data is from desert valley bottom stations where most of the scarce human habitation occurs. Billings (1954) has correlated the occurrence of juniper-pinyon woodlands in northwestern Nevada to thermal belts. This led us to suspect that the breadth of the woodland belt all across the northern portions of the Great Basin is at least partially related to the strength of development and persistence of thermal belts. Analysis of what temperature data that do exist (Fig. 17) shows a strong relationship of fewer degree-days below freezing indexes

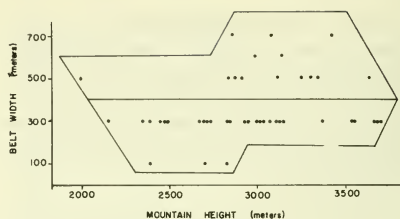


Fig. 14. Average woodland belt width (in nearest 100 m increments) in relation to maximum mountain height.

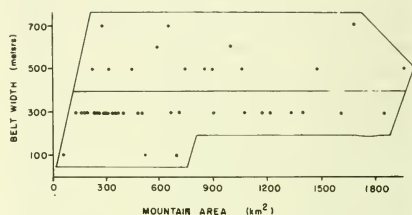


Fig. 15. Average woodland belt width (in nearest 100 m increments) in relation to mountain area above the lower boundary of woodland.

Average woodland elevational belt width

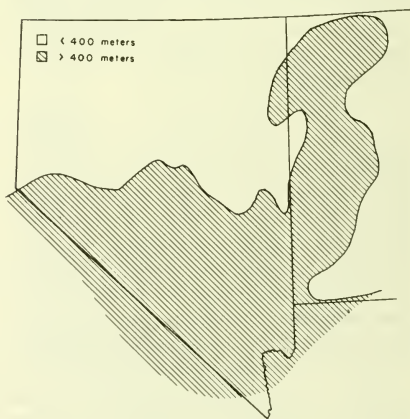


Fig. 16. Division of the Great Basin on the basis of mountain ranges having an average woodland belt width of greater or less than 400 meters vertical extent.

for meteorological stations within the woodland belt, except in the southeastern Great Basin (Pioche and Ursine, Nevada). Degree days above freezing are much higher in most woodland areas than those in the valley bottoms where various cold-winter, semidesert shrub-dominated vegetation types occur.

Juniper-pinyon woodlands are nearly absent north of Interstate Highway U.S. 80 across northwestern Nevada. Critchfield and Allenbaugh (1969) noted the correspondence of the northwestern limits of *Pinus monophylla* with the southern boundary of pluvial Lake Lahontan and speculate as to the lake being a possible barrier to plant migration. The occurrence of pinyon pine on the Virginia and Stillwater Ranges and the frequent invasion of juniper in areas that were once under the pluvial lakes of the Great Basin makes this seem unlikely. The correspondence of lakes to the pools of cold air and/or lower precipitation now in these basins seems more of an etiological factor in present distribution patterns.

Arlo Richardson (personal communication) has mapped the progression of late winter and early spring chill-unit (Richardson, Seeley, and Walker 1974) accumulations across the Great Basin. The valleys of northwestern Nevada have the most rapid progression and resultant ending of winter plant dormancy of any area in the Great Basin. Warming periods are, however, more dramatically punctuated by cold periods brought by Pacific Frontal storms there than elsewhere. This knowledge, combined with existing knowledge of air circulation and storm patterns summarized by Houghton (1969), leads us to speculate that a primary reason for the narrowing and absence of the woodland belt in the north, in addition to the latitudinal decrease in solar input, is due to the increased frequency of Pacific frontal winds breaking thermal inversions. This pattern is thought to encourage earlier plant growth but greater subsequent susceptibility of plants to direct frost damage or frost drought in a manner

similar to that found for other conifers (Hocker 1956, Newnham 1968). Supporting evidence of the net effect on woodland trees can be seen on space photography where the most northerly and westerly of the mountain ranges in the Great Basin are devoid of pinyon and juniper. In the north central portion of Nevada, ranges such as the Santa Rosa's are almost devoid of conifers altogether (Critchfield and Allenbaugh 1969). Ranges to the south and east of the ranges devoid of the woodland contain one or both tree species, implying a lee protection effect, e.g., Spruce Mountain, the southern Ruby Mountains, and the southern most tip of the East Humboldt Range (Fig. 18).

In the southern Great Basin the westerly fronts have lost most of their energy; thus their disruptive effect on the development and maintenance of thermal belts is not as frequent. Furthermore, most of the precipitation in the southern Great Basin comes from the moist Gulf air masses with rainfall triggered by the lows aloft. As a consequence, there are weaker adiabatic lapse rates (decrease in temperature with elevation) and a corresponding smaller increase in precipitation with elevation because of reduced orographic effects. For example, on the west slope of the White Mountains, the

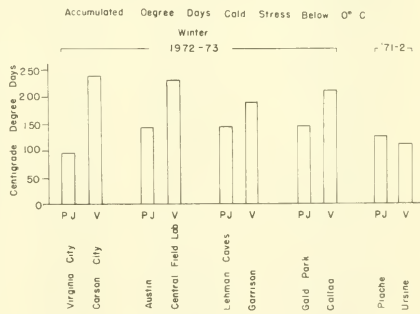


Fig. 17. Accumulated degree days cold stress below 0°C for selected woodland (PJ) and valley floor (V) climatic stations across the Great Basin (west on left, east on right). Data obtained from U.S. Weather Service climatic summaries for years indicated.

change in precipitation with elevation over the entire woodland belt is only 10 cm (4 inches) (St. Andre et al. 1965).

Although west slopes are usually the most mesic and diverse in the Basin, the woodlands on some of the mountain ranges in our study areas have higher floristic richness on the eastern and southern slopes (Table 4). This apparent reversal of the usual trend is believed to be due to the effects of nearby ranges creating rain shadows and other orographic effects. For example, in the Silver Peak Range most of the moisture must come from lows aloft positioned to the north and east. Johnson (1956) noted that the woodland belt on the south and eastern sides of the nearby Kawich Mountains had the most breadth, highest cover, and largest trees, providing corroborative evidence of this situation.

In the southern two-thirds of the study area, the lower boundary of woodlands appear to be more controlled by precipitation than temperature. Degree day values for Pioche and Ursine, Nevada (Fig. 17), are an example of how heat sums do not differ between foothill, woodland, and valley stations

in the southeast. In fact, the situation may be slightly reversed over that of the more northerly and westerly pairs of stations.

Further evidence of the interaction of temperature and moisture may be observed in the variation of the width of the woodland belt as related to mountain symmetry. Generally, the north-south axes of Great Basin mountain ranges are longer and the highest peaks are also usually in the center (Lustig 1969). When the range is protected to the west (e.g., Table Mountain in the Monitor Range) (Fig. 19), the widest belts are in the wider, higher, central east-west axis; and the belt-width decreases and average elevation increases toward the north and south ends. This is an apparent response to the Merriam effect of the greater mountain mass intercepting more moisture at a similar elevation. Extra high mountains such as Arc Dome in the Toiyabes (Fig. 19) appear to effect excessively cold, wet conditions for woodland development and the high, central axes have narrower, lower belts primarily on western slopes under such circumstances.

We have ignored here the short-term suc-

TABLE 4. Number of species (and number of stands) on each aspect of selected ranges in a west to east belt.

						Average	
Mountain Range	N	E	S	W	Total	per stand	
Western Half	Virginia	35 (2)	17 (1)	27 (2)	— (—)	50 (5)	19
	Pine Nut	32 (2)	28 (2)	23 (2)	32 (2)	57 (8)	18
	Clan Alpine	21 (2)	15 (1)	— (—)	— (—)	28 (3)	12
	Desatoya	19 (1)	20 (1)	15 (2)	28 (2)	47 (6)	15
	Shoshone	98 (13)	106 (17)	108 (22)	78 (7)	159 (59)	25
	Toiyabe	19 (1)	30 (3)	23 (2)	46 (3)	75 (9)	15
	Monitor	43 (2)	31 (3)	29 (3)	34 (2)	68 (10)	17
Average	38.1	35.3	37.5	43.6	69.1	17.1	
Eastern Half	Upper Snake	8 (1)	17 (2)	10 (2)	9 (2)	27 (7)	7
	SNAKE	10 (1)	23 (2)	11 (1)	25 (2)	49 (6)	12
	Deep Creek	31 (2)	16 (2)	17 (2)	24 (2)	49 (8)	14
	Pilot	30 (2)	21 (2)	13 (2)	26 (3)	50 (9)	12
	Needle	55 (13)	53 (16)	33 (15)	43 (12)	92 (56)	9
	WahWah	20 (2)	19 (2)	17 (2)	16 (2)	45(8)	10
	Mineral	23 (4)	18 (4)	31 (5)	32 (4)	62 (17)	9
	Stansbury	13 (1)	23 (2)	12 (1)	— (—)	37 (4)	12
Tushar	32 (2)	17 (2)	18 (2)	9 (1)	48 (7)	10	
Average	26.3	22.9	18.7	23.3	52.0	10.1	

cessional changes that are known to be operating in these woodlands. If we plot by aspect, relative tree cover, richness, and relative equitability against elevation for an example mountain range (Fig. 20), we see that richness is minimal in the closed woodlands in the middle of the belt where understory has been largely excluded by high relative tree cover. Equitability patterns are more complicated.

The approach to equitability used measures how evenly the existing total cover is divided among the species present. For each different total cover and species number a different maximum equitability is possible. To make an equitability comparison between areas of different cover and density, it is necessary to convert the figure to a relative one; in this case the percent of the maximum possible for each site. During succession (West et al. 1975) invasion by juniper and pinyon shifts in relative cover toward more trees. However, before a significant drop in total species number oc-

curs, equitability drops. As tree suppression substantially reduces the number of understory species, equitability rises. Equitability is thus highest at either end of the sere and lowest in the intermediate seral stages. This is contrary to the linear model for xeric forests proposed by Auclair and Goff (1971).

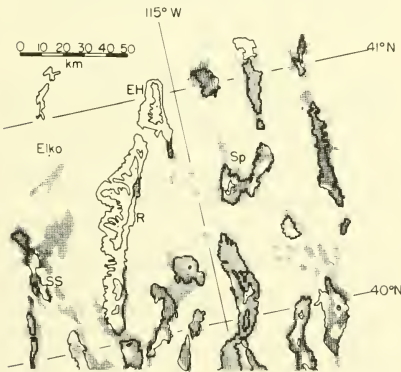


Fig. 18. Effects of exposure to westerly winds and storm tracks on occurrence of the woodland belt at the northern boundary of the type in northeastern Nevada. Stippled area is juniper-pinyon woodland, outer (lower) line is 2134 m (7000 ft.) contour, inner (higher) line is 2743 m (9000 ft.) contour. Dots are major mountain peaks: SS = Sulphur Springs Range, EH = East Humboldt Range, Sp = Spruce Mountain, R = Ruby Mountains. (Vegetation map derived from LANDSAT-1 photography. Elevational contours from U.S. Geological Survey maps.)

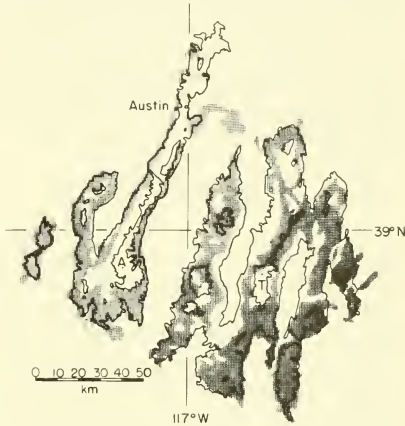


Fig. 19. Interactions of exposure to westerly storm tracks, mountain height, and mountain mass on the variation in woodland belt width and elevation in west-central Nevada. Stippled area is juniper-pinyon woodland. Outer (lower) line is 2134 m (7000 ft.) contour. Inner (higher) line is 2743 m (9000 ft.) contour. Dots are major mountain peaks: A = Arc Dome in the Toiyabe Range, T = Table Mountain in the Monitor Range. (Vegetation map derived from LANDSAT-1 photography. Elevational contours from U.S. Geological Survey maps.)

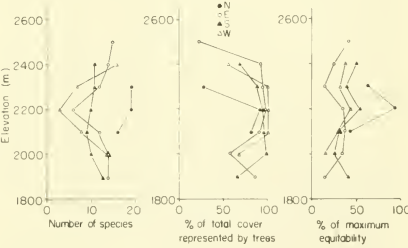


Fig. 20. Species density (floristic richness), relative percent of total cover contributed by trees, and percent of maximum equitability calculated by the McIntosh (1967) index plotted by elevation and aspect, Needle Range, Beaver-Iron Cos., Utah.

In general, the north slopes at any elevation have a larger number of species, a lower percent relative cover of trees, and a higher equitability value than the other three aspects.

Higher average diversity values were obtained in our data by including some of the woodland that is encroaching on shrublands and grasslands both above and below the main woodland belts. These successional considerations are sufficiently complex that details have to be considered elsewhere (Nabi 1978).

IMPLICATIONS

Our observations of these broad phyto-geographical patterns in Great Basin juniper-pinyon woodlands will hopefully lead to some testable hypotheses about eco-physiological responses of juniper and pinyon. For instance, what are relative evapo-transpirative and photosynthetic limits of juniper and pinyon in regard to temperature and moisture? Does needle number on pinyon relate to effective soil moisture? What are the tolerances of seedlings to temperature and moisture extremes compared to those of the mature trees? Are there late winter-early spring low temperature susceptibilities? Research to answer these questions provoked by our synecological results will be necessary to confirm our hunches.

The distributional and phytosociological variation observed within the type indicates that effective environments are radically different across the Great Basin. For the time being we can only inferentially conclude from the phyto-geographical evidence that climate is a major factor influencing the latitudinal, longitudinal, and altitudinal extent of Great Basin juniper-pinyon woodlands. Climate is also probably a greater determinant of internal floristic diversity than migrational and evolutionary equilibria. Regarding the mountains and their woodlands as islands in a uniform "sea" of desert leads to dangerous basic conclusions and confounds management application, since cli-

matic patterns are so different in the various portions of the Great Basin. These differences are striking even at the same elevation on different portions and aspects of the same mountain range. This is especially evident in data from the Shoshone Range. In general, such differences are most pronounced in the Mojave-Great Basin transition area. Stratification of landscapes into units of some homogeneity for management purposes must take these phyto-geographical patterns into account, if confusion is to be avoided.

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PATTERNS OF AVIAN GEOGRAPHY AND SPECIATION IN THE INTERMOUNTAIN REGION

Ned K. Johnson¹

ABSTRACT.—The Intermountain Region comprises a huge arena where major avifaunas more highly developed beyond the Great Basin come into contact. For this reason the distribution and composition of avifaunas in riparian and pinyon-juniper woodlands and in coniferous forests in this region are understood most clearly if considered as part of a broader system of patterns evident in western North America. Riparian woodland samples point to a complex meeting ground in the Intermountain Region of two major avifaunas of equivalent size, but from opposite distributional backgrounds. These northern and southern avifaunas do not mix among the samples represented except in western Nevada where two species of ultimate southern origin have penetrated a basically northern avifauna. Approaching the Great Basin, from the two centers of abundance of riparian species in the Snake and Colorado River drainages, species richness drops. Habitat depletion and, to a lesser extent, insularity play roles in this impoverishment. In the most depauperate riparian avifaunas, six species commonly coexist, each in a different family. Comparison of the pinyon zone avifaunas of two groups of mountain ranges, 90 km apart along the California-Nevada border, demonstrates a striking trade off among species of northern and southern biogeographic histories. The northern or Boreal forms, many of which are numerous in the Sierra Nevada, have had easy access to the favorable, cool, and relatively moist pinyon forests in the adjacent spur ranges. In contrast, the species of southern or Austral derivation prefer the warm and very arid pinyon woodland a short distance to the south. Few species are confined to either northern or southern sites, overlap in species composition is great, and equivalent species richness is achieved. However, despite these similarities, strong geographic differences in abundance of most species in each pinyon avifauna and the occurrence of at least 12 specific and subspecific range boundaries suggest the interposition between northern and southern pinyon areas of a substantial, but as yet poorly characterized, climatic barrier. Boreal species richness declines abruptly from high values in the southern Cascades and Sierra Nevada to low levels in a zone of impoverishment across western and central Nevada. From near 116° W Longitude in eastern Nevada, coincident with the appearance of fir and/or bristlecone pine forests, species numbers climb gradually until the main Rocky Mountains are reached. There, species richness compares favorably with that in the Sierra Nevada. The proportion of species favoring riparian woodlands over coniferous forests is higher on the island mountaintops of the Great Basin than in the Boreal "continents" of the Sierra Nevada-Cascades and Rocky Mountains. The western edge of the Great Basin richly demonstrates examples of stages in avian speciation. A full range of interactions is represented, from intergradation of poorly characterized races, through abrupt zones of hybridization between strongly marked subspecies of different racial complexes or of semispecies, to sympatry and infrequent interbreeding of closely-related, full species in recent secondary contact. These various zones of population interaction coincide strikingly with sharp floristic and climatic gradients. A major avifaunal break occurs between coastal or Sierra Nevada forms that inhabit oak-chaparral and/or coniferous forest and closely-related interior forms that prefer pinyon-juniper or aspen-willow associations. In keeping with the special requirements of each species, contact zones and areas of disjunction show general, rather than precise, coincidence in the western Great Basin. There is no Great Basin Boreal Avifauna; the most distinctive interior forms occur across the entire span from eastern California to Colorado. The low desert trough along the east side of the Sierra Nevada that divides major mountain systems in the western portion of the Intermountain Region is not the principal barrier dividing coastal Sierra Nevada from interior avifaunas. Instead, the major avifaunal transition occurs in a belt of variable width just east of the crest of the Cascade Mountains and Sierra Nevada, where the precipitation shadow and continental climate begin to exert crucial influence.

Although much neglected in the past because of difficulty of access and false impressions of biotic sterility, the Inter-

mountain Region of western North America is emerging as a fascinating natural laboratory requiring the close attention of the

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biogeographer-ecologist. Islands of conifers or aspen, cool mountain meadows, and attendant biotas on scores of mountaintops lie isolated by seas of desert from source stocks in the Sierra Nevada and Rocky Mountains. The unique physical setting of a multiplicity of more or less parallel ranges, each differing in size, geology, and configuration from adjacent ones, cannot be duplicated elsewhere among continental mountain systems. And, because of low human density, many of the montane habitats are relatively undisturbed, thus permitting a good look at original, man-unmodified distributions of species. In the valleys as well, oases offer insular environments for a variety of organisms whose interrupted ranges intrigue the biogeographer.

With increased field efforts by a number of workers in recent decades, the bird species breeding on many of the major basin ranges have been tallied, and information has reached a level allowing tests of certain fundamental theories of insular biogeography (Johnson 1975). However, these tests are just the beginning. With additional "alpha" exploration in the future, the enlarged data base will permit more diverse and detailed kinds of analyses. But, already enough distributional information has accumulated to suggest several patterns that challenge the avian geographer. In this paper I identify and discuss these patterns in a search for common biogeographic themes. Furthermore, I specify among the birds of the Intermountain Region distributional situations relevant to hypotheses on the control of range boundaries. Finally I describe the prominent zone of active speciation in the western part of the region and attempt to interpret this zone in relation to coincident physiographic, climatic, and floral discontinuities.

Nomenclature and sequence of species follow the checklist of North American birds except where superceded by the 32nd supplement (American Ornithologists' Union 1957, 1973).

AVIFAUNAL TRANSECTS IN THE INTERMOUNTAIN REGION

Riparian woodlands in valleys and canyons, pinyon woodlands on mountainsides, and coniferous forests and aspen on mountaintops comprise the major habitats for birds in the region between the axis of the Sierra Nevada-Cascade Range and the Rocky Mountains. Analyses of the richness and composition of selected avifaunas breeding in sample areas of these woodlands and forests expose several patterns that elucidate the fundamental organization of avian distribution in the region. Moreover, these samples along transects demonstrate the complex modes by which historical aspects of avifaunal distribution influence present-day patterns of species richness and community structure. Figure 1 shows the location of the sample areas and their basic avifaunal relationships.

Latitudinal Variation in Riparian Woodland Avifaunas

Bird species requiring riparian vegetation for breeding occur discontinuously in cottonwoods, willows, ashes, and associated thickets along watercourses and at valley oases throughout the Great Basin region. When species of land birds breeding in such habitats are compared (Table 1), among 11 sample areas from the Snake River drainage in the north to the Colorado River drainage in the south, prominent differences and some unexpected similarities emerge in total species numbers, composition of the avifaunas according to evolutionary derivation, and structure of the avifaunas by ecologic roles. That these three topics are interrelated will become evident in the discussion to follow.

Total species numbers.— Of immediate interest is the striking similarity of the geographically extreme stations, Central Idaho and Colorado River, in species richness, 28 versus 25, from the pool of 43 species. But, upon entering the Great Basin from the Snake River drainage, species totals drop, to

21 in the Elko sample, 17 in Humboldt, 15 in Toiyabe, and to 12 in Kawich. Similarly, moving north from the Colorado River, total species numbers fall to 13 in Pahrnagat, 12 in Meadow Valley Wash, and 11 at Ash Meadows-Pahrump. Figure 2 demonstrates the strong and abrupt avifaunal attenuation

that occurs with increasing distance from the lush riparian woodlands to the north and south. The smallest tallies, for the Kawich area and Ash Meadows-Pahrump, probably reflect habitat impoverishment in view of the limited extent and interrupted growth of the riparian clumps there. For

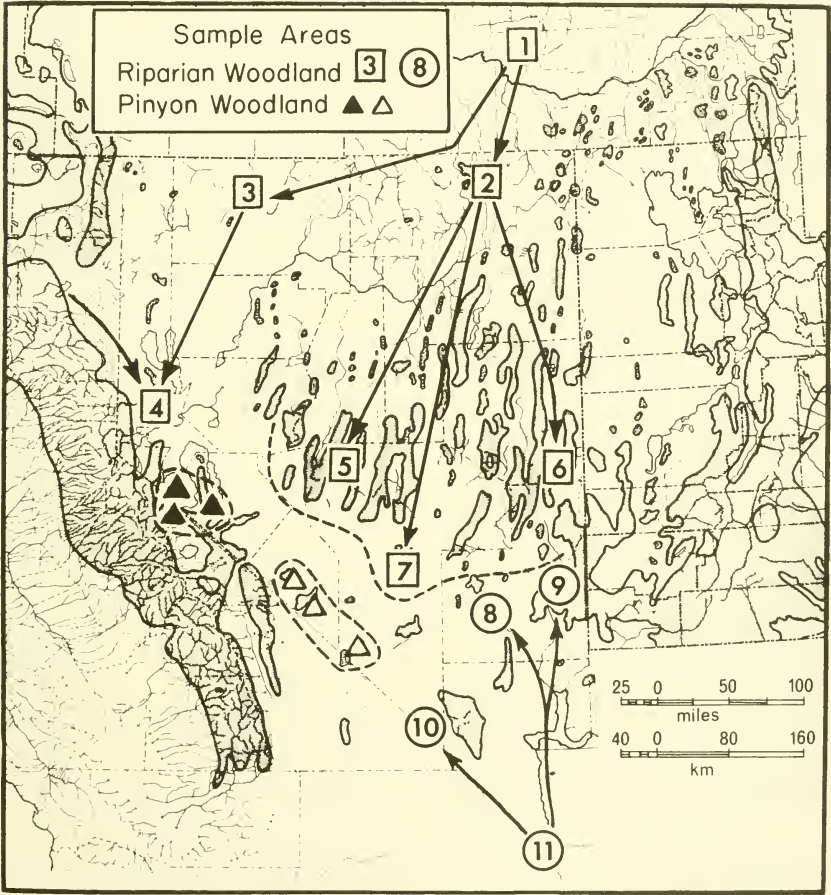


Fig. 1. Sample areas of riparian woodland (squares and circles) and pinyon woodland (triangles) avifaunas in the Intermountain Region. Shading grossly defines regions of forest and woodland. Numbers in squares or circles correspond to those of sample areas in Table 1. Arrows indicate closest avifaunal relationships. Northern and southern pinyon areas are denoted by solid and open triangles, respectively. Approximate boundary of northern and southern riparian woodland avifaunas is shown by the dashed line between samples 7 and 8.

TABLE 1. Species breeding in riparian woodlands at selected localities in the Intermountain Region¹.

	1	2	3	4	5	6	7	8	9	10	11
	Central Idaho	Elko	Humboldt	Truckee-Carson	Toiyabe	Ely	Kawich	Pahranagat	Meadow Valley Wash	Ash Meadows-Pahrump	Colorado River
Northern Element											
<i>Coccyzus erythrophthalmus</i>	X	—	—	—	—	—	—	—	—	—	—
<i>Dendrocopos villosus</i> ²	X	X	X	X	X	X	X	—	—	—	—
<i>Dendrocopos pubescens</i> ²	X	X	X	X ³	—	X	—	—	—	—	—
<i>Tyrannus tyrannus</i>	X	—	X	— ⁴	—	—	—	—	—	—	—
<i>Iridoprocne bicolor</i>	X	X	—	X	—	X	—	—	—	—	—
<i>Parus atricapillus</i> ²	X	X	—	—	—	—	—	—	—	—	—
<i>Troglodytes aedon</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Dumetella carolinensis</i>	X	—	—	—	—	—	—	—	—	—	—
<i>Turdus migratorius</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Catharus fuscescens</i>	X	X	—	—	—	X	—	—	—	—	—
<i>Catharus ustulatus</i>	X	X	X	X	X	X	—	—	—	—	—
<i>Vireo gilvus</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Vireo olivaceus</i>	X	—	—	—	—	—	—	—	—	—	—
<i>Vermivora celata</i>	X	X	X	—	X	X	—	—	—	—	—
<i>Oporornis tolmiei</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Setophaga ruticilla</i>	X	—	—	—	—	—	—	—	—	—	—
<i>Passerella iliaca</i>	X	X	X	X	X	X	—	—	—	—	—
Southern Element											
<i>Zenaidura macroura</i>	—	—	—	—	—	—	—	— ⁴	—	— ⁴	X
<i>Dendrocopos scalaris</i> ²	—	—	—	—	—	—	—	X	X	—	X
<i>Centurus uropygialis</i> ²	—	—	—	—	—	—	—	—	—	—	X
<i>Sayornis nigricans</i>	—	—	—	—	—	—	—	X	X	—	X
<i>Pyrocephalus rubinus</i> ²	—	—	—	—	—	—	—	X	—	X	X
<i>Thryomanes bewickii</i> ²	—	—	—	X ³	—	—	—	X	X	X	X
<i>Toxostoma dorsale</i> ²	—	—	—	—	—	—	—	—	—	X	X
<i>Sialia mexicana</i>	—	—	—	X ³	—	—	—	—	—	—	—
<i>Phainopepla nitens</i> ^{2,5}	—	—	—	—	—	—	—	— ⁵	—	— ⁴	X
<i>Vireo bellii</i>	—	—	—	—	—	—	—	—	—	X ⁴	X
<i>Vermivora luciae</i>	—	—	—	—	—	—	—	— ⁵	X	—	X
<i>Icterus cucullatus</i>	—	—	—	—	—	—	—	—	X	X	X
<i>Piranga rubra</i>	—	—	—	—	—	—	—	— ⁵	—	X	—
<i>Guiraca caerulea</i>	— ⁵	—	—	—	—	—	—	X	X	X	X
<i>Pipilo aberti</i>	—	—	—	—	—	—	—	—	X	—	X
Widespread Element											
<i>Falco sparverius</i> ²	X	X	X	X	X	X	X	X	X	X	X
<i>Coccyzus americanus</i>	X	—	—	X	—	—	—	X	—	X	X
<i>Otus asio</i> ²	X	—	—	X	—	—	—	X	X	—	X
<i>Archilochus alexandri</i>	X	X	—	X	—	X	—	X	—	—	X
<i>Colaptes auratus</i> ²	X	X	X	X	X	X	X	—	X	—	X
<i>Tyrannus verticalis</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Empidonax traillii</i>	X	X	— ⁵	X	— ⁵	—	—	—	—	X	X
<i>Dendroica petechia</i>	X	X	X	X	X	X	X	—	—	—	X
<i>Icteria virens</i>	X	X	X	X	X	X	X	X	—	—	X
<i>Icterus galbula</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Melospiza melodia</i> ²	X	X	X	X ⁴	X	X	X	X	—	— ⁵	X
TOTALS	28	21	17	22	15	19	12	13	12	11	25

¹Sources of data on occurrence as follows: (1) Central Idaho, a composite list from several localities in the center of the state, taken from Burleigh (1972); (2) Elko, a composite list from field notes and specimens in the Museum of Vertebrate Zoology (= MVZ) from the northern portion of Elko County, and from Linsdale (1936); (3) Humboldt, from Taylor (1912); (4) Truckee-Carson, a composite list from original data of author (= NKJ) and from Linsdale (1936); (5) Toiyabe, from Linsdale (1936); (6) Ely, data from Spring and Steptoe valleys, NKJ; (7) Kawich, NKJ; (8) Pahranagat, NKJ and MVZ; (9) Meadow Valley Wash, NKJ and Linsdale (1936); (10) Ash Meadows-Pahrump; (11) Colorado River, NKJ and Grinnell and Miller (1944). Species that typically prefer or require riparian woodland are included.

²Permanently-resident species.

³Form shows closest affinity to populations in California, to the northwest.

⁴Former or casual occurrence.

⁵Recorded during the breeding period, but not proved to be nesting.

Ash Meadows-Pahrump and Pahrnatag samples, we also may be seeing the effects of insularity. Several Colorado River drainage species, such as the Abert's Towhee (a highly sedentary, permanently resident form), probably have had great difficulty colonizing the isolated riparian areas to the north. However, one could also argue that this and other potential colonists are missing from these remote areas because the proper kinds of riparian habitats, as found along the Colorado River and its tributaries, are lacking.

The moderate size (22 species) of the Truckee-Carson sample reflects its position at the well-watered eastern base of the Carson Range.

Origin of riparian woodland avifaunas.—The entire riparian woodland avifauna can be divided on the basis of evolutionary

background or derivation into (1) a northern element consisting of species with northern centers of distribution and affinities, (2) a southern element comprised of species with southern distributional relationships, and (3) a widespread element including species occurring throughout the western United States or beyond. The species are grouped in Table 1 according to these three elements. Note that none of the species of the northern element occurs in any samples south of Kawich and, with one exception (see below), none of the species of the southern element is found in any samples north of Meadow Valley Wash or Pahrnatag. Therefore, the two major avifaunas approach, but do not contact and intermix, in the southern Intermountain Region.

Although basically of northern derivation, the riparian avifauna of the Truckee-Carson sample is of special interest because it contains a distinctive group of four species with affinities to populations of northeastern California. One of these species, the Downy Woodpecker, is of northern affinity; two species, the Western Bluebird and Bewick's Wren, are of southern derivation. The Song Sparrow is widely distributed. The western Nevadan populations of these four species probably originated from stocks in the Central Valley of California, stocks that spread into the western Great Basin via the Modoc Plateau.

The widespread component comprises between 39 and 62 percent of each sample (Fig. 2). No clear evidence of differential decline of northern (or southern) versus widespread elements is shown as the zone of impoverishment is approached. Thus, the diminution is general and involves approximately equivalent shrinkage of the two major components of each avifauna.

Community structure and ecologic roles.—A surprising finding is that the widespread species fraction seems to have stabilized, at either seven or five species, for the five sample areas with the smallest numbers of species. Thus, the Humboldt, Toiyabe, and Kawich samples have seven widespread spe-

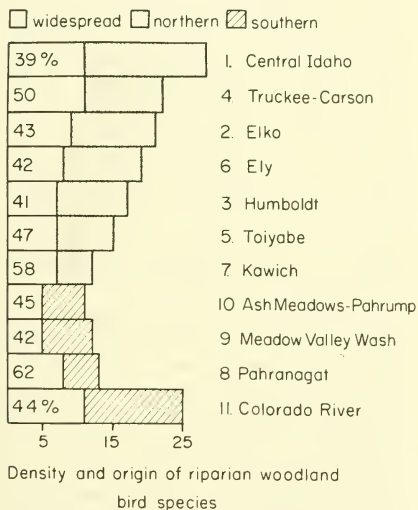


Fig. 2. Percent composition, according to geographic derivation, of avifaunas in 11 riparian woodland sample areas. These are arranged in order of decreasing avifaunal size (species density) toward the boundary of northern and southern avifaunas, between Kawich and Ash Meadows-Pahrump. For example, the Colorado River sample has 25 species, 11 (= 44 percent) of which are widespread and 14 (= 56 percent) of southern derivation.

cies in addition to northern ones. And, the lists of species are identical! The Ash Meadows-Pahrump and Meadow Valley Wash samples include southern species and five that are widespread. However, in these two samples the coincidence in identity of widespread forms is incomplete; each shares three of their five species.

Six of the 11 widespread species, *Falco sparverius*, *Colaptes auratus*, *Tyrannus verticalis*, *Icteria virens*, *Icterus galbula*, and *Melospiza melodia*, occur in nine or more sample areas. Because these species commonly coexist, they form a group of great interest. I view them as a "standard riparian woodland species" group analogous to the "standard Boreal species" group I identified in montane habitats of the western United States (Johnson 1975). Note that each of the six species is in a different family. Therefore, coexistence in the riparian woodland avifaunas examined here predominates among species of fundamentally different body designs.

Included in the tallies of Table 1 are five pairs of closely related species, three pairs of which are congeneric. Furthermore, within each pair, each species is from a different distributional element. The pairs are *Coccyzus erythrophthalmus*, and *C. americanus*, *Dendrocopos pubescens* and *D. scalaris*, *Tyrannus tyrannus* and *T. verticalis*, *Troglodytes aedon* and *Thryomanes bewickii*, and *Dendroica petechia* and *Vermivora luciae*. Not all of the species of each pair contact locally, but the interactions of those that do meet would merit close study. Indeed, a fertile field awaits the ecomorphologist willing to analyze community structure, foraging roles, and morphologic adaptations among the coexisting species of birds in any of the riparian woodlands discussed.

Latitudinal Variation in Pinyon Woodland Avifaunas

Among arboreal habitats, groves of single-leaf pinyon (*Pinus monophylla*) comprise the most extensive formation in the Inter-

mountain Region, and these woodlands therefore represent an important habitat for breeding birds. Typically this pine is scattered over mountain slopes in open stands or clumps of small trees with much intervening brush. Occasionally, on favorable sites, growth can be luxuriant, and true forest is achieved. Here trees grow to heights of 10 m or more, and the closed canopy shades a needle-strewn forest floor. This site-to-site variability in growth form of pinyon intrigues the ornithologist because, as has long been known, birds clearly respond to physical features of vegetation. A second noteworthy aspect of pinyon is the wide elevational range often occupied on a single mountainside. In the White Mountains, California, for example, pinyon occurs from approximately 2000 to 2900 m, with the best development between 2450 and 2600 m (St. Andre et al. 1965).

In the Grapevine Mountains of southern Nye County, Nevada, these variable characteristics of pinyon are seen clearly (Miller 1946). Small, scrubby trees grow in scattered stands, exceptionally fine tracts of old trees with trunks two feet in diameter form forests locally on the high northeast slopes, and the pinyon zone is wide, extending to 2650 m at the top of the highest peak. The breeding avifauna has responded to these differences. The complement of species that normally lives in pinyon of usual form and spacing is present, and several kinds of birds that typically avoid this plant formation breed in the most luxuriant stands. Evidently the latter species are attracted to physiognomic features of the pinyons that resemble those of the coniferous forest they ordinarily inhabit. Furthermore, at least three additional species that otherwise would be absent occur in the cool upper reaches of the zone, apparently responding there to preferred or required summer temperature regimes. I also have noted similar occurrences of birds in unusually dominant pinyon woodland in the Kawich Mountains of central Nye County, 100 km north-northeast of the Grapevines (Johnson 1956).

In recent years I have explored additional areas of heavy pinyon that invite avifaunal comparison with the groves in the Grapevines. These stands of old trees grow locally, in Nevada near the California line, in the Palmetto Mountains (= Mount Magruder plus the Silver Peak Mountains), Esmeralda County; the Wassuk Range, Mineral County; the Pine Grove Hills, Lyon County; and in the Sweetwater Mountains, Douglas and Lyon counties. In each of these regions, open woodlands of small trees and stands of intermediate height and density predominate on most slopes; the forests are more local in distribution.

For purposes of comparison of the avifaunas, it is useful to consider these several pinyon areas as comprising (1) a northern subset occupying the spur ranges connected to the east side of the Sierra Nevada, which includes the Wassuk and Sweetwater mountains and the Pine Grove Hills, and (2) a southern subset of wooded islands lying to the southeast, including the Palmetto and Grapevine mountains. The massive White Mountains lie between the two groups. The northern and southern subsets (Fig. 1) permit comparison of avifaunas along a northwest to southeast gradient. Some striking differences in avifaunal composition and numerical relationships of species emerge (Table 2). Although the northern and southern localities are only 90 km apart, several species reach their distributional limits between these mountain systems and thus breed in only one of the two regions. Unexpectedly, 19 species change in average population density along the gradient. For some (e.g., *Empidonax wrightii*), the change is subtle. For others (e.g., *Vireo solitarius*) population densities are dramatically different between northern and southern mountains.

Several species partly or completely share habitats. For example, *Thryomanes bewickii* and *Otus asio*, common and uncommon residents, respectively, in the pinyon woodlands of the southern Great Basin and northern Mojave Desert, prefer riparian

cottonwoods and willow in west-central Nevada. Although both species use pinyon at the more northerly sites, the wren is uncommon, and the owl is rare in this association. *Empidonax wrightii* nests in tall sagebrush, bitterbrush, and juniper in the northwestern Great Basin where pinyon is lacking but is scarce or absent in such vegetation in southern Nevada. In other species the habitat change is more subtle. *Parus inornatus* and *Dendroica nigrescens* inhabit pinyon in both northern and southern localities, but their numbers diminish in the north where they prefer the more arid and warmer portions of the pinyon belt. In 5 of the 19 species, the change in density between north and south coincides with a shift in subspecific status and, in 3 species, with a concurrent change in habitat preference (Table 2).

How are we to interpret these contrasts in the avifaunas of the pinyon association of closely adjacent geographic regions? Two interrelated issues, (1) variation in the climatic aspects of the pinyon zone environment and (2) temperature-moisture preference and distributional histories of the bird

TABLE 2. Species composition and numerical relationships of pinyon woodland avifaunas of spur ranges of the northern Sierra Nevada¹ versus those of montane islands to the southeast². Boreal (B) and Austral (A) species are distinguished.

Species present only in north:	
<i>Glauclidium gnomus</i> ³ (B)	<i>Certhia familiaris</i> ³ (B)
<i>Sphyrapicus ruber</i> ³ (B)	<i>Myadestes townsendi</i> (B)
<i>Cyanocitta stelleri</i> (B)	
Species present in both areas but more numerous in north:	
<i>Agelaius acadicus</i> (B)	<i>Sialia currucoides</i> (B)
<i>Dendrocopos villosus</i> ⁴ (B)	<i>Piranga ludoviciana</i> (B)
<i>Tachycineta thalassina</i> (B)	<i>Carpodacus cassinii</i> (B)
<i>Parus gambelii</i> ^{4,5} (B)	<i>Chlorura chlorura</i> (B)
<i>Sitta carolinensis</i> (B)	<i>Junco hyemalis</i> (B)
Species present in both areas but more numerous in south:	
<i>Otus asio</i> ^{4,5} (A)	<i>Thryomanes bewickii</i> ^{4,5} (A)
<i>Empidonax wrightii</i> ⁵ (A)	<i>Poliophtila caerulea</i> ⁵ (A)
<i>Aphelocoma coerulescens</i> (A)	<i>Vireo solitarius</i> (B)
<i>Psaltiriparus minimus</i> ⁴ (A)	
Species present only in south:	
<i>Regulus calendula</i> ³ (B)	<i>Icterus parisorum</i> (A)
<i>Vireo vicinior</i> (A)	<i>Junco ciniceps</i> (B)

¹Wassuk Range, Sweetwater Mountains, and Pine Grove Hills.

²Grapevine Mountains and Palmetto Mountains (= Mt. Magruder + Silver Peak Mountains).

³Breeds only very locally in pinyon woodland in the northern or southern mountains.

⁴Subspecies in north different from that in south.

⁵Partial or complete habitat shift from north to south.

species at northern and southern stations, may offer partial explanation.

From rainfall data for the nearby White Mountains and several other pinyon sites in the southwest, St. Andre et al. (1965) concluded that overall aridity characterizes this plant formation. Unfortunately, no moisture data exist for the pinyon zones in the ranges of special interest here. Nonetheless, pinyon certainly occupies a range of rainfall regimes, and the more northern sites, although still relatively arid, presumably have greater average rainfall than the southern sites. Temperature data also are scarce, except for the White Mountains. However, I can conclude at least that the upper part of the zone averages considerably cooler than the lower part, a fact readily apparent to the researcher working at different elevations in this region. The unusual upper extension of the pinyon zone in the White Mountains (St. Andre et al. 1965) and in the Grapevine Mountains (Miller 1946) would enhance temperature differences that normally exist between the different elevations. Finally, because of the difference in latitude, it is probable that the northern sites average cooler than the southern ones.

The climatic preferences and distributional backgrounds of the bird species agree closely with the groupings of Table 2. The 5 species confined to the north and all 10 forms that are more numerous in the north are Boreal species with distributional backgrounds associated with northern coniferous forests. In contrast, except for *Regulus calendula*, *Vireo solitarius*, and *Junco caniceps*, forms of Boreal derivation (Miller 1951), all the species present only in the south or reaching their greatest numbers in the southern pinyon areas are of Austral origin, having been associated in their distributional histories with southwestern pinyon or oak woodlands. I conclude that this major trend in composition and density of pinyon zone avifaunas along the Nevada-California border apparently results from the exchange along a temperature-moisture gradient of southern pinyon woodland species, adapted

principally to the warm and relatively arid portions of the zone, and northern species, adapted chiefly to the relatively cool and moist portions of the zone.

The origin of the bird species of the Wassuks, Sweetwaters, and Pine Grove Hills is of particular interest because the pinyon woods in these ranges directly contact the coniferous forests of the Sierra Nevada. For this reason, bird populations of the pine-fir zone of the east side of the latter range have had easy access to pinyon forests lying to the east. Ready access may be one reason why *Cyanocitta stelleri* and, locally, *Certhia familiaris* and *Sphyrapicus ruber* breed in pinyon in these areas. Otherwise these species are not known to nest in this formation. It is noteworthy that none of these forms inhabits the old pinyon groves in the Desatoya Mountains of central Nevada, presumably because of the great distance of this range from source populations.

Note that from the pool of 27 pinyon zone species, nearly identical total numbers of breeding forms, 23 and 24, respectively, are recorded for northern and southern stations. Such equivalence is significant. Importantly, no neat system of replacement or of switches in abundance by species with similar ecologic roles occurs along the gradient (Table 2). Instead, the evolution of community structure at various localities in the pinyon formation probably has involved more subtle adjustments among the species in foraging zones, food quality, and/or habitat preference. Those species of birds represented by different geographic races at northern and southern localities would be especially worthy of close study in this regard.

Gradients in Boreal Avifaunas

I recently discussed controls of richness of Boreal species on 11 sample areas in the Sierra Nevada, Cascades, and Rocky Mountains and on 20 mountaintop islands in the Intermountain Region (Johnson 1975). Here I wish to expand on portions of that analysis through examination of both longitudinal and latitudinal trends in numbers of species

occupying particular Boreal habitats along four transects across the Great Basin. These transects (Fig. 3, lines I-IV) are roughly equidistant latitudinally and pass through 20 of the sample areas described in my previous paper. Species numbers now have been determined for eight additional areas, and these new data are included. Transect III fails to cross the entire Intermountain Region because no species lists are available for restricted portions of the main Rocky Mountains directly east of the Snake Range in eastern Nevada.

Total species richness.— All transects demonstrate the abrupt drop in total numbers of species in the north-south-oriented swath that extends across much of western and central Nevada (Fig. 4A). From high species totals of 56 to 64 at Mt. Shasta,

Lassen, Tahoe, and Yosemite, species richness declines sharply along transect I, between Warner and Pine Forest; along transect II, between Lassen and West Humboldt; along transect III, between Carson and Pine Nut; and along transect IV, between Yosemite and Glass Mountain. Species numbers then climb toward the east to totals of 56 and 55 at Uinta and Aquarius-Boulder, respectively, at the ends of the transects. Highest totals for the Sierra Nevada-Cascades always equal or exceed those for the Rocky Mountains. In the region of general impoverishment along each transect, a mountain range moderately rich in Boreal species interrupts the general smoothness of each species density curve (Fig. 4A): I, Jarbidge; II, Ruby; III, Toiyabe-Shoshone; and IV, White-Inyo.

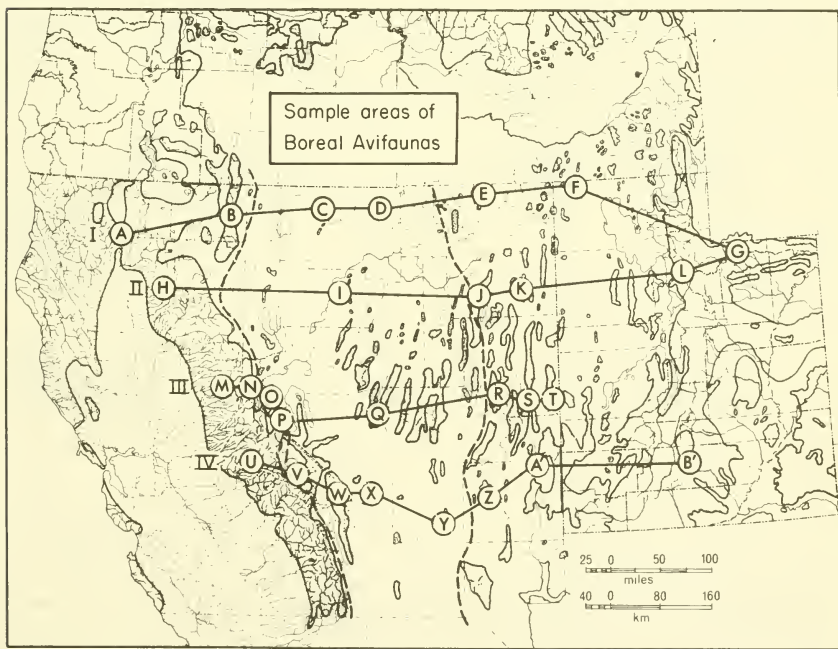
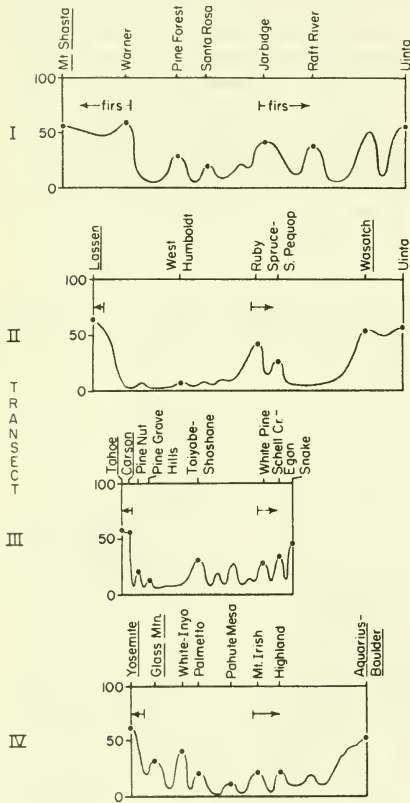


Fig. 3. Four transects across the Intermountain Region, passing through 28 sample areas of Boreal avifaunas. These sample areas are named in Fig. 4. No native firs are known to occur between the two vertical dashed lines.

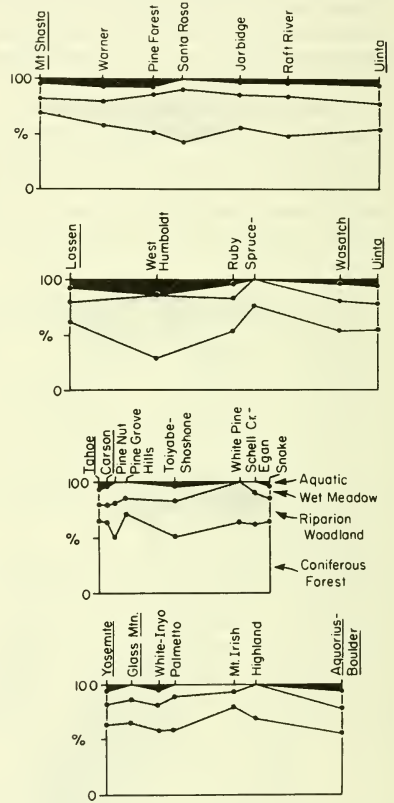
Species richness according to habitat.— In Figure 4B I portray the percentage of Boreal species in each of four major habitats (Johnson 1975: 549), i.e., Aquatic, Wet Meadow, Riparian Woodland, and Coniferous Forest. This permits study of possible changes along gradients of proportions of species preferring these habitats. For

each transect I have calculated the average percentage of species in each of the four habitats for Sierra Nevada-Cascades samples, Great Basin Islands samples, and Rocky Mountains samples (Table 3).

Between-transect comparisons of proportions of species in continental samples indicate striking similarities. For example,



A. Boreal bird species richness



B. Composition of boreal avifaunas

Fig. 4. Numbers of Boreal bird species (left) and percent avifaunal composition by four major habitats (right) along four transects across the Intermountain Region. Continental sample areas are underlined; island sample areas are not. Twenty sample areas are described more fully in Johnson (1975). Species totals for eight new ones added are as follows: A, Mt. Shasta (Grinnell and Miller 1944); I, West Humboldt Range (author's unpubl. data); L, Wasatch (Behle and Perry 1975); M, Tahoe (Orr and Moffitt 1971); O, Pine Nut Mtns. (author's unpubl. data); R, White Pine Mtns. (author's unpubl. data); S, Schell Creek-Egan Ranges (author's unpubl. data); and Y, Pahute Mesa (Hayward et al. 1963).

number of species in coniferous forests varies only from 62.5 to 69.6 percent of the total Boreal avifauna in the Sierra Nevada-Cascades, and those of riparian woodland vary only from 23.2 to 24.6 percent in the several samples from the Rocky Mountains. Other habitats on continents illustrate similar uniformity. Island samples are more complex and show differences among transects. Specifically, the island samples of transects I and II have proportionately more aquatic and riparian woodland species, but fewer coniferous forest species, than those of transects III and IV.

Within-transect comparisons (transects I, II, and III) point to more riparian woodland species and fewer coniferous forest species in samples for the Great Basin Islands versus the Sierra Nevada or the Rocky Mountains. However, the ecologic preferences of

birds in island samples resemble those of birds in Rocky Mountains samples more than those of forms in the Sierra Nevada-Cascades. The avifaunas of transect IV do not follow the pattern of the first three in that the proportions of species in the several major habitats are similar among samples of the Sierra Nevada, Great Basin, and Rocky Mountains.

The composition of coniferous forest avifaunas.— The fraction of coniferous forest bird species deserves special comment because some of the trends in total species richness discussed earlier are explained partly by the distribution of suitable tree species. The following group of forest bird species, distributed discontinuously in the Intermountain Region, illustrates this point: *Sphyrapicus varius*, *Sphyrapicus thyroideus*, *Empidonax hammondi*, *Empidonax difficilis*,

TABLE 3. Average percent composition, according to habitat preferences, of species in avifaunas along transects.

	SIERRA NEVADA-CASCADES CONTINENT (Mt. Shasta)	GREAT BASIN ISLANDS (Warner through Raft River)	ROCKY MOUNTAINS CONTINENT (Uinta)
Transect I			
Aquatic	3.6	3.7	5.3
Wet Meadow	12.5	10.8	16.1
Riparian Woodland	14.3	34.0	23.2
Coniferous Forest	69.6	51.5	55.4
		(W Humboldt through Spruce-S. Pequop)	(Wasatch and Uinta)
Transect II	(Lassen)		
Aquatic	7.8	6.3	3.6
Wet Meadow	12.5	4.0	17.3
Riparian Woodland	17.2	37.1	24.6
Coniferous Forest	62.5	52.6	54.6
		(Pine Nut through Snake)	
Transect III	(Tahoe and Carson)		
Aquatic	4.4	0.9	—
Wet Meadow	14.8	10.8	—
Riparian Woodland	16.5	27.4	—
Coniferous Forest	64.4	60.9	—
	(Yosemite and Glass Mountain)	(White-Inyo through Highland)	(Aquarius- Boulder)
Transect IV			
Aquatic	2.3	0.6	3.7
Wet Meadow	12.3	7.0	14.5
Riparian Woodland	19.0	23.4	23.6
Coniferous Forest	66.4	69.0	58.2

Sitta canadensis, *Certhia familiaris*, *Regulus satrapa*, *Regulus calendula*, *Hesperiphona vespertina*, and *Spinus pinus*. Although most of these forms occasionally breed in other kinds of conifers or in deciduous trees, they prefer firs (*Abies concolor* or *Pseudotsuga menziesii*) and avoid or nest sparingly in forests lacking these trees. Thus, the distribution of firs in the Intermountain Region is of special significance for these species. Figure 4A indicates the presence of firs in the various sample areas. Note the repeated instances of increased numbers of species, of all kinds of birds and of coniferous forest birds, in relation to the appearance of firs.

Firs are absent from the zone of avifaunal impoverishment across western and central Nevada (Fig. 3). Although skimpy clumps grow in the Sweetwater Mountains, no fir occur in any of the other ranges along the California-Nevada border southeast of the Carson Range. Firs reappear in eastern Nevada between 115° and 116° W Longitude. Among the ranges considered here, substantial stands occur in the Jarbidge Mountains, White Pine Mountains, and on Mount Irish. Critchfield and Allenbaugh (1969) report white fir locally in the Ruby Mountains, but the avifauna at that site has not been explored.

Bristlecone pine (*Pinus longaeva*) dominates the upper slopes of several ranges in eastern Nevada. This tree is important for coniferous forest birds in part because it occasionally forms closed, well-shaded stands with strong physiognomic resemblance to firs. Apparently in response to this feature, several kinds of birds from the above list often occupy well-developed bristlecone pine forests when firs are scarce or lacking. The two species of *Sphyrapicus*, *Empidonax difficilis*, *Sitta canadensis*, and *Regulus calendula* exemplify this point. In Nevada, the best stands of this conifer grow east of the right vertical dashed line on Figure 3 that marks the boundary of white fir distribution, and in many places the two species occur in mixed stands.

BREEDING RANGE BOUNDARIES AND INTERSPECIFIC DISTRIBUTIONAL RELATIONSHIPS

Broad trends in avian geography are best identified through comparison of major components of avifaunas. Other, more detailed issues can be seen most clearly by inspection of the distributions of single species and their close relatives. Here I discuss four contrasting examples, chosen from a long list of possible cases, that illustrate particular species-level distributional phenomena occurring among birds of the Intermountain Region. Three of these examples also support the view offered earlier that this region presently serves as an important arena of disjunction, contact, and intermixture of species representing avifaunas of differing geographic derivation.

Grace's Warbler and ponderosa pine.—In southeastern Nevada, as in the southern Rocky Mountains generally, Grace's Warbler (*Dendroica graciae*) breeds commonly and exclusively in forests of ponderosa pine (*Pinus ponderosa*). But near the northwestern edge of the occurrence of the Rocky Mountain form of the ponderosa pine (*P. ponderosa* var. *scopulorum*), for example in the Quinn Canyon Range, the scattered and stunted trees occupy marginal sites, and the bird is rare. It is absent from the few ponderosas that grow locally in the Highland Range, on Mount Wilson, and in the southern White Pine Mountains, and, farther north, from the extensive ponderosa pine habitat in the Snake Range (Fig. 5).

This case is particularly interesting because prior to 1963 the Grace's Warbler was not known to breed anywhere in southern Nevada. Since then, numerous records have been obtained, several from places that previously had been well-explored (Johnson 1965, 1973, 1974). Therefore, the evidence points to an active northwestward range expansion in the past decade or two. Although further extension into presently unoccupied ponderosa pine habitat is possible, total distributional evidence suggests

that the approximate northwestern limit in the Intermountain Region already has been reached. However, given continued range expansion, eventual colonization of the arid ponderosa pine forests of southern California seems probable, for the species is already vagrant to that area, and a number of other species of the interior Southwest have become established there in recent years (Johnson and Garrett 1974). Insofar as is known, Grace's Warbler has never nested in the vast ponderosa pine forests of the central and northern Rockies, or in the Sierra Nevada.

The warbler thus illustrates two biogeographic phenomena typically seen in species with well-documented distributions: (1) the actual range falls short of the geographic extent of seemingly appropriate habitat and (2) the distributional boundaries are unstable because of their complex con-

trol by a multiplicity of interacting factors that are themselves fluctuating. I wish to emphasize that no other species of warbler or other pine-foliage insectivore obviously competes with *D. graciae* and, for this reason, has adjusted its distribution and abundance as a result of recent population interaction with that species. Instead, the northwestern distributional perimeter of Grace's Warbler seems to be set by other aspects of the environment. For example, this warbler may be dependent upon populations of pine arthropods that fluctuate in annual density, especially near the periphery of their ranges. Or, summer temperature and moisture barriers dictated by the metabolic requirements and preferenda of the warbler, the arthropods upon which it feeds, or the pines they both inhabit, may control the range border. I have no data to support a convincing explanation.

Downy Woodpecker and Ladder-backed Woodpecker in disjunct allopatry.— These two congeners fail to contact in the Great Basin. The Downy inhabits aspen groves in the northern and eastern mountains (the form *D. p. leucurus*), or cottonwoods and willows along rivers in west-central Nevada (the form *D. p. turati*), and the Ladder-back lives in the cottonwood-willow association in valleys or Joshua tree woodland in the Mojave Desert. Unexpectedly, substantial areas of apparently suitable habitat occur in the wide zone now unoccupied by either species. Thus, the Downy Woodpecker has not been found in the fine aspen woodland in the Schell Creek Range or on Mount Wilson, among a number of seemingly appropriate places. Similarly, the Ladder-back avoids considerable Joshua tree growth in Esmeralda and Nye Counties, Nevada. Finally, neither species breeds in the excellent riparian woods in Owens Valley, although the Ladder-back has been recorded at Lone Pine, at the foot of the valley (Grinnell and Miller 1944). I conclude that the respective southern and northern limits of these two species, within suitable habitats, are dictated primarily by temperature and mois-

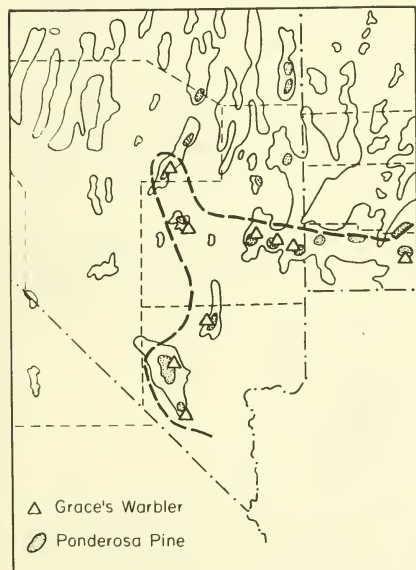


Fig. 5. Approximate breeding distribution of Grace's Warbler (triangles) and occurrence of ponderosa pine (stippled areas) in southeastern Nevada and southwestern Utah. Lower elevational perimeters of woodlands in mountains also are indicated.

ture. Considering the wide unoccupied swath between their ranges in the central Intermountain Region, distributional limits there certainly are not controlled by interspecific competition.

Mountain Bluebird and Western Bluebird in parapatry.— These two congeneric thrushes (*Sialia currucoides* and *S. mexicana*, respectively) breed in contiguous allopatry, or parapatry, in much of the southern Intermountain Region. One might conclude that such a distributional relationship is the result of interspecific competition (Fig. 6). In at least three general areas where both species have been recorded (Panamint Range, Delamar Range, Zion National Park), their spatial relationships are unclear. But, because of their well-known differences in habitat preference (Grinnell and Miller 1944), competitive interaction probably is infrequent or absent, given a situation of local sympatry. Until more details are available, I conclude that the striking parapatry results from the geographic position of a

sharp shift in average spring and summer temperatures. The approximate coincidence of the zone of parapatry with the northern limits of the Mojave Desert supports this suggestion.

Hammond's Flycatcher and Western Flycatcher in broad sympatry.— As in the previous examples, this case also concerns a species of northern derivation, Hammond's Flycatcher (*Empidonax hammondi*), and a congener of southern derivation, the Western Flycatcher (*E. difficilis*). These two forms offer a particularly impressive example of how the complex interplay of phylogenetic and distributional history has influenced present-day habitat selection and ecologic interaction. Figure 7 shows the distributional and numerical relationships of these species in western North America.

Hammond's Flycatcher is commonest in cool, moist Boreal forests of the Sierra Nevada, Cascades, and Rocky Mountains; its principal range therefore surrounds the Intermountain Region on three sides. In con-

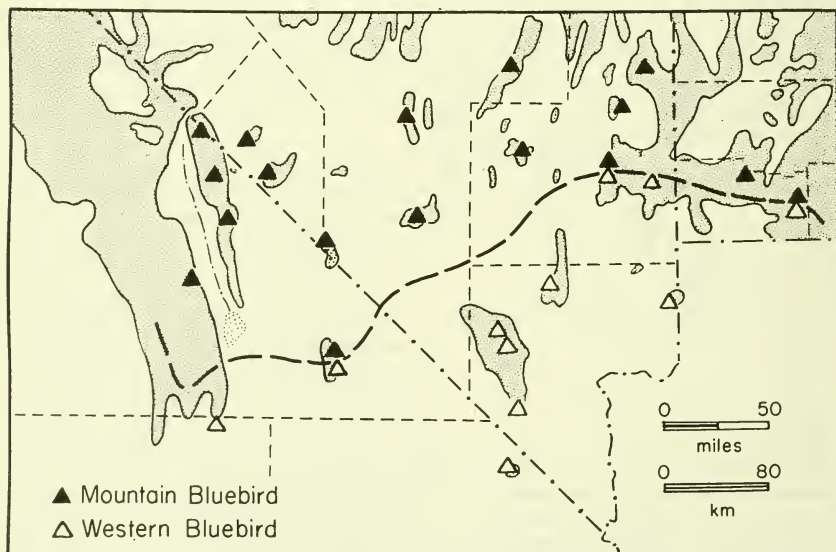


Fig. 6. Breeding distributional relationship of the Mountain Bluebird (*Sialia currucoides*) and Western Bluebird (*S. mexicana bairdi*) in southern Nevada and adjacent states.

trast, the Western Flycatcher reaches its greatest densities in warm Pacific Coastal forests (small form *E. d. difficilis*) and in arid interior highland forests of the Intermountain Region and southern Rocky

Mountains of Arizona and New Mexico (large form *E. d. hellmayri*), where *E. hammondii* is either absent or rare and local. In areas of contact between Hammond's Flycatcher and the similarly sized *E. d. diffi-*

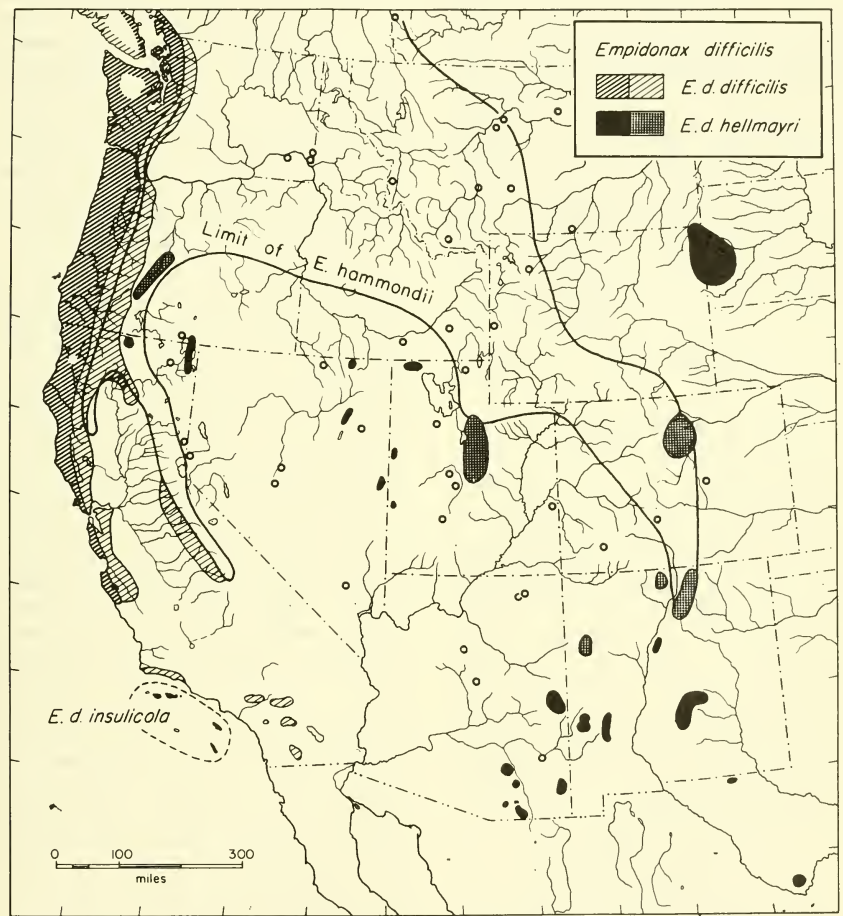


Fig. 7. Breeding distributional relationship of Hammond's Flycatcher (principal range outlined) and Western Flycatcher in the contiguous western United States. Relative abundance of three forms of Western Flycatcher is shown by patterns as follows: *E. d. difficilis*, heavy slanted lines indicate very common to abundant populations, and light slanted lines indicate common to uncommon populations; *E. d. hellmayri*, black indicates very common to abundant populations, and dotted pattern indicates common to uncommon populations. *E. d. insulicola* is common to abundant on the California Channel Islands, indicated in black. Scattered localities for *E. d. hellmayri* are shown by circles; note that many of them occur within the main range of *E. hammondii*. A few localities for the latter species, located south of the main range, are omitted.

cilis in the Pacific Northwest and on the west side of the Cascades, interspecific territories are defended (Johnson 1966 and unpubl. data). In the Rockies of southern Colorado the larger *E. d. hellmayri* evidently overlaps in territories with *E. hammondi* (Beaver and Baldwin 1975). The important point is that these two species are largely allopatric; considering the bulk of their numbers, this results directly from selection of similar, though not identical, habitats in different major climatic zones. Where they overlap, one species is nearly always common, the other uncommon or rare. Despite the geographic shifts in relative abundance and subtle differences in habitat selection, which presumably are consequences of millennia of competitive interaction, the two species do occur sympatrically in many places. Obviously one species has not limited the geographic range of the other (Fig. 7).

Within the genus *Empidonax*, these two species are separated phylogenetically by a series of other forms of closer relationship. The Hammond's Flycatcher is allied to the Least Flycatcher (*E. minimus*) and to other species of Boreal derivation (Johnson 1963). The Western Flycatcher, in contrast, is closest to Neotropical montane stocks such as *E. flavescens* and is certainly of southern derivation (N. K. Johnson, unpubl.). Apparently such evolutionary backgrounds have permitted extensive convergence in habitat preference and foraging ecology, for in the western United States, *E. hammondi* and *E. difficilis* are the commonest *Empidonax*es of dense coniferous forest.

Controls of Boundaries of Species' Ranges

The previous accounts offer only the barest introduction to the vast subject of the determinants of borders of breeding distributions of birds. Nonetheless, it is appropriate to comment briefly on this topic because it lies at the heart of biogeography and because of significant trends in the pertinent literature.

Grinnell (1914, 1917) and Bartholomew (1958), among others, have emphasized manifold controls of distributional boundaries of animal species, with the importance of particular factors changing along the range perimeter. They favored niche requirements and physiologic-climatic preferences as the crucial dictates of species distributions; interspecific competition either was not mentioned or its relevance was subordinated. In the more recent literature of ornithological ecology, the limitation of geographic range through competitive exclusion has become a prominent theme (MacArthur 1972, Cody 1974). However, the invocation of competition in this context has been premature.

In agreement with Salt (1952), whose classic paper clearly describes how metabolism and climate interrelate to control the distributions of three species of finches (*Carpodacus*), I see little reason to postulate competition as an effective determinant of range borders of species of birds in the Intermountain Region. The question is not whether competition occurs among the many overlapping species here; rather, it is what form does this competition take, and, as such, can it influence range boundaries? From all the evidence I have seen, including that from the four examples discussed, competition probably has had little influence in the determination of range boundaries of birds. Instead, alterations in density, such as shown for the two species of *Empidonax*, are the more likely outcomes of competitive interactions. Finally, I suggest that it is unwise to conclude that boundaries of tropical species are set by competition (Terborgh and Weske 1975), in the virtual absence of data on the occurrence of those environmental requisites crucially related to the distribution of the bird species in question.

PATTERNS OF AVIAN SPECIATION IN THE INTERMOUNTAIN REGION

In this section I concentrate on what I consider to be active zones of speciation in

the Great Basin region. These are illustrated by currently interacting populations of closely related taxa, well-differentiated at various levels above that of the incipient subspecies. For those concerned with more subtle examples of racial differentiation in this region, Behle (1963) provides a useful review. Information on speciation zones is of significance to the data previously presented on avifaunal gradients because of the great probability that the same environmental discontinuities in climate and flora ultimately are responsible for both.

Zones of Intergradation, Disjunction, and Secondary Sympatry

Birds demonstrate a particularly wide range of speciation phenomena along the western edge of the Great Basin, in a zone extending south-southeastward from southern Oregon to southeastern California and southern Nevada. Indeed, there is evidence from the general distribution and speciation of birds in western North America that the zone just delineated is actually part of a larger biotic separation that extends northward to British Columbia and beyond. Here I wish to discuss 16 selected pairs of taxa (Table 4) in the western Intermountain Region that illustrate stages in the speciation process. Figure 8 schematically portrays zones of intergradation and hybridization for nine of these pairs of taxa.

Several patterns emerge from study of this wealth of material. The first concerns the striking, although imprecise, geographic coincidence of the several contact zones that link (or divide) coastal and interior populations. Secondly, a large number of species are represented, suggesting that significant environmental gradients or discontinuities in the western Great Basin pervasively influenced the differentiation of birds. Indeed, few other regions in North America can claim a comparable diversity of speciation phenomena within such restricted geographic limits.

Furthermore, the interacting taxa of nearly every pair occupy different habitats

on each side of the contact zone (Table 5). Habitats in the contact areas themselves are typically intermediate between coastal and interior situations. In a major trend illustrated by six pairs of taxa, the coastal representative inhabits coniferous forest or oak

TABLE 4. Examples of coastal or Sierra Nevada and interior taxa that illustrate speciation phenomena along the interface of the Cascades-Sierra Nevada and Great Basin.

Gradual primary integradation; racial boundaries weak¹:

1. *Sphyrapicus thyroideus thyroideus* and *S. t. nataliae*. Williamson's Sapsucker.

Narrow zone(s) of primary or secondary intergradation between representatives of strongly divergent racial complexes:

2. *Empidonax difficilis difficilis* and *E. d. helmayri*². Western Flycatcher.
3. *Eremophila alpestris sierrae* and *E. a. lamprochroma*. Horned Lark.
4. *Aphelocoma coerulescens superciliosa* and *A. c. nevadae*. Scrub Jay.
5. *Psaltriparus minimus californicus* and *P. m. plumbeus* or *P. m. providentialis*. Bush-tit.
6. *Amphispiza belli canescens* and *A. b. nevadensis*. Sage Sparrow.
7. *Passerella iliaca megarhynchus* and *P. i. fulva* or *P. i. monoensis*. Fox Sparrow.
8. *Dendrocopos pubescens turati* and *D. p. leucurus*. Downy Woodpecker.

Disjunct allopatry between representatives of strongly divergent racial complexes:

9. *Parus inornatus inornatus* or *P. i. kernensis* and *P. i. zaleptus*. Plain Titmouse.
10. *Vireo solitarius cassinii* and *V. s. plumbeus*. Solitary Vireo.
11. *Vermicora celata lutescens* and *V. c. orestera*. Orange-crowned Warbler.

Narrow zone or sympatry and interspecific hybridization:

12. *Sphyrapicus ruber daggetti*. Red-breasted Sapsucker and *S. varius nuchalis*. Red-naped Sapsucker.
13. *Junco hyemalis thurberi*. Dark-eyed (Oregon) Junco and *J. caniceps caniceps*. Gray-headed Junco.

Disjunct allopatry between species:

14. *Pica nuttalli*. Yellow-billed Magpie and *P. pica hudsonia*. Black-billed Magpie.
15. *Vermicora ruficapilla ridgwayi*. Nashville Warbler and *V. virginiae*. Virginia's Warbler.
16. *Leucosticte tephrocotis dawsoni*. Gray-crowned Rosy Finch and *L. atrata*. Black Rosy Finch.

¹Many additional examples of this category could be cited (see Behle 1963).

²In each pair of taxa the coastal-Sierran form precedes the interior form.

TABLE 5. Habitat preferences and contact zones of taxa listed in Table 4.

SPECIES 1	HABITAT OF COASTAL ² OR SIERRAN FORM	HABITAT OF INTERIOR FORM	ZONE(S) OF CONTACT OR APPROACH OF TAXA	SOURCE
1. Williamson's Sapsucker	Mixed coniferous forest.	Mixed pine-fir, especially white fir- bristlecone pine.	Warner Mtns. area.	N. K. Johnson (1970).
2. Western Flycatcher	Canyon-bottom woodlands or forests in lowlands and foothills.	Riparian woodlands or forests in high- lands.	Siskiyou Mtns. area.	N. K. Johnson, unpubl.
3. Horned Lark	Large mountain meadows surrounded by conifers.	Playas surrounded by sparse desert scrub.	Sierra Valley, Plumas Co., Calif.	Behle (1942).
4. Scrub Jay	Oak woodland and chaparral.	Pinyon-juniper woodland.	Douglas Co., Nev.; E slope southern Sierra Nevada in Inyo Co., Calif.	Pitelka (1951).
5. Bush-tit	Evergreen oak-chaparral.	Pinyon-juniper and mountain mahogany woodland.	Lassen Co., and E slope southern Sierra Nevada, Inyo Co., Calif.	Grinnell, Dixon, and Linsdale (1930); Swarth (1914).
6. Sage Sparrow	Mixed brushland of <i>Artemisia</i> with much <i>Atriplex</i> .	Sagebrush scrub; some <i>Atriplex</i> .	Mono Co., Calif.	Grinnell and Miller (1944).
7. Fox Sparrow	Brushland of <i>Ceanothus</i> and <i>Arctostaphylos</i> . Less commonly, riparian thickets.	Riparian thickets of willows, aspens, birches, and alder; less commonly, brushland.	Modoc-Lassen Cos., and Alpine-Mono- Inyo Cos., Calif.	Grinnell and Miller (1944).
8. Downy Woodpecker	Willows and cottonwoods in lowlands and foothills.	Aspen and cottonwoods in mountains.	Modoc Plateau.	Grinnell and Miller (1944).
9. Plain Titmouse	Oak woodland.	Pinyon-juniper woodland.	No known contact; ranges divided by Sierra Nevada.	Grinnell and Miller (1944).

10. Solitary Vireo	Dry and warm conifer and oak forests.	Pinyon-juniper woodland.	No known contact. Forms approach to within 50 km in vicinity Alpine Co., Calif. and Lyon Co., Nev.	N. K. Johnson, unpubl.
11. Orange-crowned Warbler	Mixed oak woodland-chaparral.	Aspen woodland.	Forms approach in vicinity of Alpine Co.-Mono Co. border.	Grinnell and Miller (1944).
12. Red-breasted and Red-naped Sapsuckers	Mixed coniferous forest and woodland.	Aspen woodland; also white firs.	Warner Mtns., Modoc Co., Calif.; Mono Co., Calif. and Lyon Co. and Mineral Co., Nevada.	Howell (1952); N. K. Johnson, unpubl.
13. Dark-eyed (Oregon) and Gray-headed Juncos	Open coniferous forest with grassy openings.	Dense pinyon and/or mountain mahogany woodland with grass or herbs on shaded floor.	Mountains along state line between Mono Co. and San Bernardino Co., Calif.	Miller (1941); N. K. Johnson, unpubl.
14. Yellow-billed and Black-billed Magpies	Pasture lands with clumps of trees.	Stream and lake valleys with clumps of willow or <i>Shepherdia</i> .	No contact; ranges separated by axis of Cascades and Sierra Nevada.	Grinnell and Miller (1944).
15. Nashville and Virginia's Warblers	Oak-conifer woodland with brushy understory.	Pinyon or scrub oak woodland.	No contact; ranges approach along Calif.-Nev. border SE of Lake Tahoe.	N. K. Johnson, 1976.
16. Gray-crowned and Black Rosy Finches	Alpine cirques and meadows.	Alpine cliffs and adjacent turf.	No contact in area of this study. Absent in summer in wide swath across W and Cent. Nev.	R. E. Johnson (1975).

¹For ease of comparison, the species are listed according to the sequence of Table 4.

²The principal kind of habitat occupied in most places is described. Any form listed here may breed uncommonly or rarely in somewhat different habitats.

woodland-chaparral, and the interior race or species lives in pinyon-juniper woodland. In four additional pairs of taxa, the coastal or Sierran form occupies oak-chaparral, coniferous forest, or brush associated with such forest, and the interior form switches to riparian aspen or willows. Earlier I discussed the latter trend (Johnson 1970).

In 5 of the 16 pairs, the coastal and interior representatives are disjunct, with ranges separated by gaps that overlap or straddle many of the zones of intergradation of the 11 pairs of forms that do contact. Evidently the intervening habitat separating the disjunct forms is unsuitable for these particular species. Seven of the 11 pairs that meet and interact occur less commonly in the contact zone than in the adjacent regions. This

clearly suggests that population densities are reduced for several species in and near their zones of intergradation. Thus, the environments at the western border of the Intermountain Region are unsuitable for certain species and marginal for others. In any case, the variety of distributional and speciation phenomena represented underscores the steep environmental gradients that influence selection pressures on bird populations in the restricted zone where the Cascade Mountains and Sierra Nevada meet the Great Basin. Munz and Keck (1968), Baldwin (1973), and Miller (1951) describe the significant physiographic, floristic, and climatic changes ultimately responsible for the evolution of contrasting avifaunas in this region.

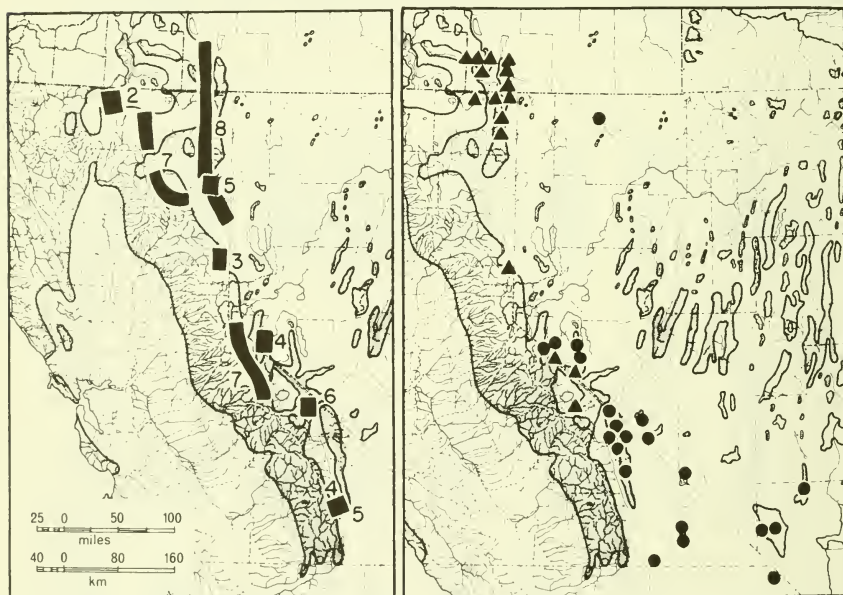


Fig. 8. Left, zones of primary intergradation and hybridization (secondary contact), at the western border of the Great Basin, in seven species of birds. Numbers correspond to those in Table 4: 2, Western Flycatcher; 3, Horned Lark; 4, Scrub Jay (two zones); 5, Bush-tit (two zones, one of which is identical with a zone of the Scrub Jay); 6, Sage Sparrow; 7, Fox Sparrow (two zones); and 8, Downy Woodpecker. Right, localities of sympatry and hybridization between Red-breasted and Red-naped Sapsuckers (triangles) and between Dark-eyed (Oregon) and Gray-headed Juncos (dots).

Physiographic Breaks and Avifaunal Boundaries

A major gap in the mountain systems of the western United States results from the low trough that begins in southeastern Oregon, courses southward through western Nevada, veers southeastward between Walker Lake and the Paradise Range, then continues through the Death Valley area and beyond into the Mojave and Colorado deserts. With such a geographic position, it would be easy to assume that this trough separates the Boreal avifaunas of the Cascades and Sierra Nevada from those of the interior. However, this is not the case, for a host of interior races and species of birds occur westward to the Warner, Wassuk, Sweetwater, and White mountains. These interior forms therefore maintain popu-

lations on the west side of the trough at localities well-removed from their principal centers of distribution from central Nevada eastward. These occurrences provide clear evidence for the suitability, for at least some interior species, of those montane environments located directly adjacent to the southern Cascades and east side of the Sierra Nevada. But these same ranges also host many Cascadian and Sierran forms that have colonized from the west. Thus, peculiarly intermixed avifaunas breed in all four mountain systems (Table 6). One of the four ranges, the Sweetwaters, has only a minor representation of interior forms; the others have numerous Great Basin-Rocky Mountain species. All of the other mountain systems along the Nevada-California border, the Carson Range, Pine Nut Mountains, Pine Grove Hills, and Glass Mountain, lack inte-

TABLE 6. Intermixture of Cascade-Sierra Nevadan and interior components¹ in Boreal avifaunas of mountain ranges² along the western edge of the Great Basin.

CASCADE MOUNTAIN-SIERRA NEVADAN FORMS	WARNER MOUNTAINS	WASSUK RANGE	SWEETWATER MOUNTAINS	WHITE MOUNTAINS
<i>Dendragapus obscurus sierrae</i>	X	—	X	X
<i>Sphyrapicus ruber daggetti</i>	X	X	X	—
<i>Cyanocitta stelleri frontalis</i>	X	X	X	X
<i>Vireo solitarius cassinii</i>	X	—	—	—
<i>Vermivora ruficapilla ridgwayi</i>	X	—	—	—
<i>Wilsonia pusilla chryseola</i>	—	—	X	—
<i>Leucosticte tephrocotis dawsoni</i>	—	—	X	X
<i>Junco hyemalis thurberi</i>	X	X	X	X
<i>Passerella iliaca monoensis</i> ³	—	X	X	—
GREAT BASIN-ROCKY MOUNTAIN FORMS				
<i>Selasphorus platycercus</i>	—	X	—	X
<i>Sphyrapicus varius nuchalis</i>	X	X	X	X
<i>Dendrocopos pubescens leucurus</i>	X	—	—	—
<i>Empidonax difficilis hellmayri</i>	X	—	—	— ⁴
<i>Vireo solitarius plumbeus</i>	—	X	X	X
<i>Vermivora celata orestera</i>	X	—	—	X
<i>Vermivora virginiae</i>	—	X	—	X
<i>Wilsonia pusilla pileolata</i>	X	—	—	X
<i>Junco caniceps caniceps</i>	—	—	—	X
<i>Passerella iliaca fulva</i>	X	—	—	—
<i>Passerella iliaca canescens</i>	—	—	—	X

¹Emphasis is on forms of contrasting Sierra Nevadan versus interior distribution. Many undifferentiated species of widespread distribution in the western United States are not considered here.

²Sources of data: Warner Mountains, Miller (1951) and Johnson (1970); Wassuk Range, original data of author and few records from Linsdale (1936); Sweetwater Mountains, specimens in MVZ and original data of author; White Mountains, Grinnell and Miller (1944) and Miller and Russell (1956).

³The avifaunal relationships of this form are uncertain.

⁴Miller and Russell (1956) report *E. d. difficilis* in late June, but the bird was not certainly nesting even though the specimen was in breeding condition.

rior forms; their Boreal avifaunas are entirely comprised of Sierra Nevadan and widespread species. Because the most distinctive interior species and racial complexes, such as *Selasphorus platycercus*, *Vermivora virginiae*, and the *woodhouseii* Group of *Aphelocoma coerulescens*, extend all the way from eastern California to Colorado, there is no Boreal avifauna typical only of the Great Basin section of the interior.

The aforementioned distributional evidence thus supports the principal conclusion derived from the location of contact zones, namely, that the most trenchant separation of coastal-Sierran versus interior stocks occurs in a zone of varying width that runs southward just east of the crest of the Cascades then southeastward along the interface of the Sierra Nevada and Great Basin. Presumably it is the beginning of the precipitation shadow and the consequent shift from a coastal to an interior continental climate that provide the profound environmental transition responsible for this zone. The low desert trough to the east does not represent a significant avifaunal barrier.

Epilogue.—Avian geography in the Inter-mountain Region continues to progress, albeit cautiously, from the descriptive to the analytic phase. With only crude patterns now discernible, much remains to be learned and interpreted. But, heeding E. O. Wilson's (1970) reminder that "...biogeography is far and away the most difficult of all the biological sciences," I am inclined to treat with great kindness even those tentative patterns that so far have surfaced from the chaos.

ACKNOWLEDGMENTS

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EXPLOSIVE EVOLUTION OF PERENNIAL *ATRIPLEX* IN WESTERN AMERICA¹

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ABSTRACT.—New habitats opened up in western North America since the recession of Lake Bonneville and Lake Lahontan have admitted a host of new species of *Atriplex*. Every known evolutionary force is operating and at accelerated paces. Autoploidy appears to be more common than in any other reported group of plants. Natural hybridization between closely related species has provided a wealth of fertile segregants from which new adaptive types have been and are being selected. Hybrids between more distantly related species are sterile and some appear to have given rise to fertile allopolyploid derivatives.

All evidence points to a center of origin for *Atriplex* in northern Mexico. The numerous species which have migrated northward into western United States and Canada were apparently able to do so because attributes acquired to make them adaptive in the hot dry deserts of Mexico were characteristics which, uniquely, also pre-adapted them for colder climates and alkaline clay soils to the north.

Woody species such as *Atriplex canescens* and *A. confertifolia* hybridize rather easily with herbaceous perennial species such as *A. cuneata*, *A. gardneri*, *A. corrugata*, and *A. obovata*. Since most such hybrids are at least partly fertile and produce F_2 segregants of both woody and nonwoody types, the genetic basis for the accumulation of wood is apparently rather simple.

According to Antevs (1955), Broecker and Kaufmann (1965), Morrison (1965), Russell (1885), and others, much of the land surface of western Utah and northwestern Nevada was covered with ice and water as recently as 10,000-12,000 years ago. During the subsequent rapid disappearance of Lake Bonneville and Lake Lahontan and the attending desertizing of surrounding valleys, numerous salt playas and alkali flats were formed. Very few plants have been capable of surviving the severe physiological drought which characterizes such habitats. Compounded by attending severe climatological drought, which in many places is nearly absolute, the number of adaptive plants and animals is even further minimized. Indeed, in many areas, islands of dry, saline, mud hills and alkali playas are still completely uninhabited. Such areas represent some of

the few last frontiers on earth yet to be exploited by living organisms.

The principal pioneers which reach out farthest into these sterile desert islands are plants belonging to the family *Chenopodiaceae*. The entire family appears to possess, uniquely, characteristics which permit the accommodation of this double challenge of physiological and climatological drought. At the borders of every sterile, empty island in these saline deserts some member of this remarkable family is at the last frontier. In bottomlands it is usually *Sarcobatus* or *Suaeda* or *Salicornia* or *Allenrolfea*. On dryer sites it is *Grayia* or *Ceratoides* or *Atriplex* or *Salsola*.

Most chenopod genera are highly specialized with very few adaptive variables. Only two species of *Sarcobatus* have been described: *S. vermiculatus* (Hook.) Torr and *S.*

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baileyi Cov. There are only two species of *Grayia*: *G. spinosa* (Hook.) Moq. and *G. brandegei* Gray. There is only one species of *Ceratoides* (*C. lanata* (Pursh) J. T. Howell) in North America and one of *Cycloloma* (*C. atriplicifolium* (Spreng.) Coult.). But, in contrast, *Atriplex* is awesomely genetically rich, consisting of numerous species and varieties, many of which are still unnamed.

Some *Atriplex* species are very narrowly endemic, others are phenomenally widespread. *Atriplex navajoensis* Hanson is confined to a restricted area near Navajo Bridge in northern Arizona, whereas *Atriplex canescens* (Pursh) Nutt. extends all the way from Montana southward, deep into Mexico. Some species such as *Atriplex garrettii* Rydb. are remarkably uniform throughout their entire distribution; others, such as *Atriplex confertifolia* (Torr. and Frem.) S. Wats. are highly flexible with numerous ecotypes, chromosome races, and subspecies.

So genetically rich is *Atriplex* in western America and so new and variable are the environs which it occupies that we are permitted to witness the evolutionary process at an unprecedented rate. Every known strategy for speciation is evident, some of which, such as autopolyploidy, have never been reported to be nearly so significant in the evolution of other plant groups.

Interspecific hybridization followed by introgression, segregation, or allopolyploidy is common; mutations, drift, and autopolyploidy are found in nearly every species. Interpretations are easy in some groups, but in others the evidences are rather subtle and difficult to interpret.

EVOLUTIONARY HOT SPOTS

Atriplex is abundant throughout all of western America. One or more of the evolutionary forces can be witnessed in nearly every population, but there are a few particular sites where speciation is especially rapid.

One of the richest evolutionary sites lies in northeastern Mexico in a radius of about

200 miles around Monterey. Here there are numerous endemic diploid and tetraploid species, and numerous hybrid derivatives. As pointed out by Johnston (1941), *Atriplex stewartii* I. M. Johnston is an apparent derivative of the hybrid *Atriplex canescens* x *A. acanthocarpa* (Torr.) S. Wats. It has thin, broad leaves with undulating margins, much like the leaves of *A. acanthocarpa*, and four-winged fruits which, although diminutive, are much like those of *A. canescens*. West of San Roberto is another segregant from this hybrid but, in this case, with *A. canescens*-type leaves and *A. acanthocarpa*-type fruits. Even another derivative from this hybrid grows in very heavy gypsum soils southwest of Cuatro Ciénegas. It is much like *A. acanthocarpa* in many respects of habit and leaf but has a strong tendency for wings on an otherwise burrlike fruit.

Atriplex prosopidium I. M. Johnston is a handsome, tall, four-winged shrub with a deep blue cast which probably came from introgression of *A. obovata* Moq. into *A. canescens*. It is narrowly endemic to a small area around Monclova and Ocampo. A much more widespread putative derivative of this same origin covers thousands of acres south and west of Cuatro Ciénegas. It is a short-statured, heavy bush, much utilized by sheep and cattle in that area.

A second geographic center in which hybridization has played, and is now playing, a major role in the origin of new species of *Atriplex* is in north central Nevada. Valleys in this region run north and south between series of mountain ranges. Each valley is approximately 30 to 60 miles across and 100 to 400 miles long and usually opens up to common basins to the north and to the south. This peculiar physiography permits species to migrate from common populations into isolated valleys where independent speciation can occur and unique species can emerge. And they have. In almost every valley unique genotypes have become established. Furthermore, fortuitous contacts between north and south immigrants as well as fortuitous in-

roductions of particular combinations of species from either the north or the south has provided many of the valleys with new rich opportunities for interspecific hybridization followed by segregation, introgression, and polyploidy.

Atriplex canescens has been particularly contributive in this setting. In western Utah and northern Nevada it has hybridized with *A. tridentata* Kuntze yielding a host of new variables. This is particularly unusual because *A. canescens* in this area is tetraploid whereas *A. tridentata* is hexaploid. However numerous viable seeds are produced by the hybrid in nature, providing a host of segregating progeny. Some of these have recovered high fertility and chromosomal regularity at the tetraploid level but are phenotypically, and therefore genetically, strongly modified by *A. tridentata*. Conversely, some segregants have settled down chromosomally at $2n = 54$ and are phenotypically like *A. tridentata*, introgressed with *A. canescens*. Still others are not yet stabilized, either genetically or chromosomally. Each of these permutations have also been obtained in the experimental nursery at Brigham Young University from seeds collected from natural hybrids.

In and around Battle Mountain, Nevada, thousands of acres are occupied by a highly variable population of *Atriplex* which appears to have been derived from this parentage. The plants are strongly *A. tridentata* in many features but tendencies for winged fruits, earlier maturation, and woodiness all suggest introgression from *A. canescens*. This population appears to have become chromosomally stabilized at 27 pairs but is still unstabilized genetically.

In many of the valleys of west central Nevada, *Atriplex canescens* appears to possess genetic attributes of *A. falcata* (M.E. Jones) Standl. Since these *A. canescens* populations are hexaploid, whereas most others in western America are tetraploid (Stutz et al. 1975), and, since *A. falcata* has so far proven to be always diploid, these hexaploid *A. canescens* populations are prob-

ably allohexaploids derived from the hybrid of tetraploid *A. canescens* x diploid *A. falcata*. The principal difficulty with this interpretation, however, is the abundant variation within these hexaploid populations. A monophyletic hexaploid origin should have provided a very uniform product. Consequently, if the parentage has been correctly interpreted, then a polyphyletic origin is required, either initially or from among partially fertile segregants of the original hybrid or else abundant continuing hybridization between the new allohexaploid and one or both of the parents, followed by subsequent introgression.

Another highly variable hexaploid population occupies extensive valleys south of Eureka, Nevada. These are much less like *A. canescens* than are those described above which occupy valleys to the west. If these, too, are allohexaploid derivatives from the hybridization of tetraploid *A. canescens* and diploid *falcata*, considerable segregation must have occurred prior to the event of chromosome doubling because these plants show a minor influence of *A. canescens* and a major *A. falcata* input.

Certainty about whether or not these are the correct interpretations must await further study and experimental breeding. But whatever the ancestry, the fact remains that these partially isolated valleys in central Nevada are hot beds of *Atriplex* evolution. Nearly every valley possesses unique genotypes. In many valleys the variation is still rampant and has not yet settled down to a predominant adaptive theme. It is an evolutionary arena in which speciation is proceeding at unprecedented rates.

Eastern Utah is another region in which both polyploidy and interspecific hybridization have furnished many new species and varieties. The most common interspecific hybrids are those derived from *A. cuneata* A. Nels x *A. canescens* and *A. cuneata* x *A. confertifolia*. The latter is highly sterile but a few segregants are to be found in nature, and I have now obtained several seedlings from many thousands of hybrid "seeds."

The hybrid *A. canescens* x *cuneata*, however, is, in some places, quite fertile and produces extensive segregating populations. Immediately west of Hanksville, Emery Co., Utah, about thirty acres is dominated by hundreds of segregants from this parentage. Since *A. cuneata* is usually a suffrutescent shrub, dying back almost entirely each year to the ground, whereas *A. canescens* is a woody shrub, accumulating wood year after year, it was interesting to find both growth forms represented among the segregants, suggesting a rather simple genetic basis for this difference.

Numerous other natural interspecific hybrids have been found in eastern Utah, e.g., *A. confertifolia* x *A. garrettii*, *A. confertifolia* x *A. corrugata* S. Wats., and *A. confertifolia* x *A. canescens*, but extensive successful segregants have not yet been noted.

Probably the most significant products of interspecific hybridization in all *Atriplex* is that produced from hybridization of *A. canescens* with *A. gardneri* (Moq.) Dietr. In northern Wyoming and southern Montana these two species are often intimately sympatric. Hybridization between them is common, attended by a rich array of segregant products. From such hybrid swarms have come several highly adaptive combinations, one of which appears to be the widespread, herbaceous form of *A. canescens* which grows in the heavy clay soils on the banks of the Missouri River and its tributaries throughout most of Montana, southern Alberta, northern Wyoming and North and South Dakota. It was this form which was collected in 1804 by Lewis and Clark at Big Bend near Chamberlain, South Dakota, and which is the type for *A. canescens*. Because of the many differences which distinguish it from the typical taller, more woody, well-known four-wing saltbush of the Intermountain West and northern Mexico, a nomenclatural revision will be required.

ORIGINS

It is difficult to be certain of the center

of origin of species in a genus as genetically rich as *Atriplex*. According to Vavilov (1926), it would be in one of the areas in which there is abundant variation. However, in *Atriplex* this may not be a good index for origins. As pointed out above, most of the evolutionary hot-spots are of very recent vintage and possess abundant variation not because of antiquity but rather because of recent availability of new explorable habitats. Also, unacceptable are theories such as those of Matthew (1939) which suggest that centers of origins can be detected by the presence of advanced, progressive species. This, too, would place the center of origin in northern Utah and Nevada or eastern Utah, where evolution is currently explosive and where, but a few thousand years ago, much of the area was covered with water.

In view of the widespread severe ecological changes during Pleistocene and Holocene in all of western America north of Mexico, in view of the numerous affinities between perennial *Atriplex* species of northern Mexico and those to the north, and in view of the numerous species in southern states and Mexico such as *A. acanthocarpa* (Torr.) S. Wats., *A. obovata* Moq. *A. polycarpa* (Torr.) S. Wats., *A. hymenelytra* (Torr.) S. Wats., and *A. torreyi* (S. Wats.) S. Wats. which have no homologues nor even analogues in northern states or Canada and also because there is a paucity of perennial *Atriplex* species south of San Luis Potosi, northeastern Mexico appears to be the most likely area from which most contemporary perennial, North American species of *Atriplex* arose. Adaptation to the hot dry climate and gypsiferous soils of this area conceivably could have preadapted many forms for occupation of the xeric saline areas which became available to the north during late Pleistocene. It may have involved biological adaptation as simple as the capacity for accumulating and tolerating salts at an unusually high concentration. Ostensibly the attending high osmotic pressure of such an adaptation could function as an "antifreeze" in colder northern climates as well as a

mechanism for accommodating drought, both physiological and climatological. No other common denominator is yet apparent.

Such an origin is also fully supported by other lines of evidence. Leaves of all perennial *Atriplex* species, so far examined, have the "Kranz" type leaf anatomy which appears to be always associated with the C_4 photosynthetic pathway (Downton 1971, Polya and Osmond 1972). Even *Atriplex falcata* which now is confined solely to northern latitudes and other diploid species as far north as Edmonton, Alberta, still display Kranz type anatomy. If, as is generally maintained, C_4 photosynthesis is an adaptation to hot, bright desert conditions, (Downton 1971, Mooney et al. 1974, Smith 1976, and others) it is difficult to accept that these northern species arose *in situ* under existing climatic conditions. However, a southern hot-desert origin for a species now completely restricted to northern climates is also difficult to accept. But if the Kranz anatomy is as reliable an index to C_4 photosynthesis as has been claimed, and if C_4 photosynthesis is as restricted to hot climate plants as has been suggested, then there are really no other available explanations. And if we accept all of that then we are forced to accept, in either case, migration and evolutionary tempos of very unusual rates. The only apparent northerly migration lanes were right through Utah and Nevada, and these were mostly under water only 10 or 12 thousand years ago. If this migration were earlier, it must have been during the interstadial between the Bull Lake and Pinedale pluvials, and the current distribution of northern species as far south as northern Nevada and Utah would be a recent subsequent southerly migration.

Since most of Alberta and Saskatchewan was completely covered with ice and water as recently as 20,000 years ago (Bayrock 1969, Christiansen 1971), *Atriplex* species which are now restricted to areas in these provinces as far north as Edmonton and Peace River must have immigrated from the south since that time. Also, since consid-

erable time would be required for the wasting and disappearance of the ice sheets, desert conditions conducive to *Atriplex* migration would not have been available until even much later. And, since most of Utah and Nevada were still mostly covered with ice and water as recently as 10,000 years ago (Bissell 1963, Morrison 1965), there are not very many time periods left in which the required major desert could have developed. In fact, it appears that there are only two possibilities: (1) about 10,000 to 12,000 years ago, just prior to the last major Bonneville pluvial or (2) about 5,000 years ago during the Altithermal period of post Bonneville. In view of the great distance which migrating species would need to traverse to get from southern deserts to far northern latitudes, plus time for radiation into the numerous existing adaptive ecotypes and *in situ* synthesis of polyploid derivatives, neither of these time intervals are particularly appealing. But since there appears to be no available alternative it must have happened during one or perhaps both of these periods. The tempo of migration and evolution would have necessarily been very rapid. But since it is very rapid today, perhaps it is not so unrealistic after all.

According to Morrison (1965), a distinct period of dessication separated the Bonneville and Draper pluvials about 12,000 years ago. It was a relatively brief period during which the Grantsville soil was deposited at levels as low as 4250 feet. This is just 50 feet above the current level of Great Salt Lake so would indicate desert conditions perhaps as severe as those existing today. Also Eardley (1962) found a huge bed of Glauber's salt ($Na_2SO_4 \cdot 10H_2O$) from 15 to 25 feet below the present-day bottom of Great Salt Lake, $9\frac{1}{2}$ miles across and 32 feet thick, the surface of which dated at $11,600 \pm 400$ years B.P. Further evidence of a major drought 10,000-12,000 years ago is furnished by cores taken from Searles Lake which show an 18-foot-thick layer of salt of that age (Smith 1962).

Increasing frequencies of *Atriplex confer-*

tifolia in wood-rat middens in the Mojave Desert beginning about 17,000 years ago (Wells 1976) may also be counted as evidence for extant desert conditions in western North America prior to the last Bonneville pluvial. Wells also furnished evidence which suggests that the Chihuahuan Desert may have originated less than 11,500 years ago. Widespread desert conditions may have lasted for only a few hundred or perhaps a few thousand years but were probably sufficiently extensive to permit *Atriplex* and other desert plants to migrate from the south.

Some of the *Atriplex* species which are now endemic to the northern latitudes are, uniquely, successfully competitive with grasses and forbs with which they grow. Elsewhere *Atriplex* is conspicuously a poor competitor and is successful on harsh sites primarily because nothing else can grow there. Consequently the northern forms have apparently become secondarily adapted for competitiveness in sites which are considerably more mesic than those occupied by other species of *Atriplex* further to the south. Since such adaptation is likely genetically somewhat complex, it probably required considerable time to arise. This is further argument that migration from the south must have occurred at an early period rather than during the Altithermal of only 5,000 to 6,000 years ago.

The pluvial period following the extant drought 10,000 to 12,000 years ago apparently wiped out all northern forms of *Atriplex* except those which were adaptively competitive with other mesophytes. At least one of these northern *Atriplex* species, near Edmonton, Alberta, is diploid so probably represents a product of primary evolution involving principally genetic drift and the acquisition of new adaptive mutations.

Considerable evidence is now accumulating which suggests that desert conditions were also widespread during the Altithermal period. Scott (1965) reports mollusks dated at 5500 B.P., buried 40 feet under eolian sand near Denver, Colorado, and Smith (1962) reports 40 feet of salt of altithermal

age deposited in Lake Searles in eastern California. Whether the warm Altithermal period developed synchronously throughout all of western America to provide one huge desert or whether deserts developed in different areas at different times is not known but neither is it critical to *Atriplex* evolution and migration. A single widespread desert would, of course, be simpler to comprehend but stepwise movement from one area to another could have been just as effective. The principle conclusion in either case is the same. *Atriplex* must have migrated from the south, over thousands of miles, across terrain which has subsequently become so modified that intervening forms have become completely extinct. Ancestral types, if they still exist, are so very different from those to the north which have evolved from them that evidences of such ancestry are not at all apparent.

Although the climate of northeastern Mexico has apparently changed very little during the past 30,000 to 40,000 years (Meyer 1973) in comparison to the tumultuous surface changes to the north, *Atriplex* growing there would have certainly continued to evolve. However, if the northern derivatives migrated from the south during the recent Altithermal period, many original ancestral types would predictably still be present. But none are to be found, a fact which suggests that migration must have been much earlier.

Wells (1966) has reported *Atriplex canescens* fossils at Burro Mesa in the Chihuahuan Desert which date at 36,000 years B.P. However, today only polyploid forms of this species have been found in Mexico (Stutz et al. 1975). The only population of diploid *Atriplex canescens* yet found is on sand dunes in central Utah and may represent the only relic stand of the ancestral form. However it is so genetically distinctive and so restricted in its distribution, it is almost certainly a derived form, considerably altered from its progenitors.

Many other diploid species of *Atriplex* scattered throughout the Intermountain

West are likewise geographically disjunct from any apparent Mexican relative. Most of them have narrow restricted distributions so were probably left behind as adaptations to unique situations during and after the migration rampage.

All of this argues strongly for greater antiquity in *Atriplex* migration than can be afforded by the Altithermal period and consequently supports other evidences for widespread desert conditions prior to the last Bonneville pluvial, of a magnitude sufficient to accommodate migration and evolution every bit as rapid as that which we witness today in the wake of new ecological sites exposed by post-Bonneville climatic changes.

As new ecological permutations now emerge, encroaching evolutionary fronts exploit them. Hence the entire Intermountain West today is once again an evolutionary arena in which new species are emerging and migrating at phenomenal rates. Mountains which are islands for mesophytes are isolation barriers for xerophytes, and the valleys which are isolation barriers for mesophytes are islands for the xerophytes. As these isolation barriers are surmounted by chance migrants, or adaptive deviants, new waves of evolutionary turbulence evoke yet other genetic permutations which accommodate even other challenges. It would be difficult to imagine a more dynamic arena wherein to witness the evolutionary process and it would also be difficult to find a genus better fitted for adaptively responding to it than *Atriplex*.

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DISTRIBUTION AND PHYLOGENY OF ERIOGONOIDEAE (POLYGONACEAE)

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ABSTRACT.—Eriogonoideae is a subfamily of the knotweed family, Polygonaceae, endemic to the New World, and is composed of 14 genera and perhaps 320 species. It differs primarily from the other members of Polygonaceae in lacking well-defined sheathing stipules or ochrea. The species of Eriogonoideae vary from tiny, fragile annuals to herbaceous perennials, low subshrubs or shrubs to large and often arborescent shrubs. The seemingly most primitive extant genus of the subfamily is *Eriogonum* (247 species), which is widespread in central North America. A series of genera are closely related to *Eriogonum*, and probably have evolved directly from *Eriogonum*. These genera are *Oxytheca* (9 species) of the western United States, and Chile and Argentina of South America; *Dedeckera* and *Gilmania*, both monotypic genera of the Death Valley region of California; *Stenogonum* (2 species) of the Colorado Plateau and adjacent areas of the Rocky Mountain West; *Goodmania* and *Hollisteria*, 2 monotypic genera of central and southern California; and *Nemacaulis*, a monotypic genus of the southwestern United States and northwestern Mexico. A second major complex of genera also probably evolved from *Eriogonum*. In this group, the most elementary genus is *Chorizanthe* (about 50 species), in which the extant perennial members of the genus are perhaps evolutionarily the oldest taxa of the subfamily. These perennials are restricted to Chile, while in the western United States and northwestern Mexico of North America, only annual species are found. *Mucronea* (2 species) of California and *Centrostegea* (4 species) of the southwestern United States and northwestern Mexico are clearly related to *Chorizanthe*. In a somewhat intermediate position between the *Eriogonum* complex and the *Chorizanthe* complex—but still more closely related to the latter than the former—is the genus *Lastarriaea* (2 species) found in California, Baja California, and Chile. All of these genera belong to the tribe Eriogoneae. A second tribe, Pterostegeae, contains only 2 discordant, monotypic genera: the shrubby perennial genus *Harfordia* of Baja California and the more widespread annual, *Pterostegia*, of the western United States. While time and evolution have obscured the relationships between Eriogoneae and Pterostegeae, the affiliations among the various genera of the tribes can be ascertained to some degree. The geographical center of origin of the subfamily may have been in a subtropical climate, with the differentiation of modern-day genera occurring in temperate, xeric regions of North America. The origin of *Chorizanthe* was an ancient development, with the migration of the primitive perennial members into South America in the Tertiary. The subsequent development of the annual habit, and migration of annual species of Eriogonoideae into South America has probably occurred in the Quaternary. The intermediate stages of evolutionary development of the genera and species of the subfamily occurred in a habitat similar to the pinyon-juniper woodlands of the Great Basin, while evolution of the more advanced genera and species has occurred in xeric grasslands, chaparral scrub, or xerophytic "hot desert" communities.

INTRODUCTION

In considering the action of evolutionary processes ... both extinction and extensive alterations of geographic and ecological distribution patterns must be recognized. (Stebbins 1974: 37).

Polygonaceae Juss. is a large, temperate or subtropical family of flowering plants found throughout much of the world, but

mainly in the Northern Hemisphere. It contains many important agricultural and horticultural species in addition to many well-known and troublesome weeds. The vast majority of the plants are small, inconspicuous members of the world's vascular plant flora, and they can claim few positive attri-

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butes. The family is composed of about 40 genera and approximately 900 species (Lawrence 1951, Melchior 1964, Airy Shaw 1973), with *Polygonum* L., *Rumex* L., *Eriogonum* Michx., *Coccoloba* P. Br. ex L., *Rheum* L., and *Chorizanthe* R. Br. ex Benth. among the larger genera in terms of species numbers. Domestically, the genus *Fagopyrum* Mill. is the commercial source of buckwheat, and leaf petioles of *Rheum* (rhubarb) are frequently eaten. *Antigonon* Endl. is an elegant ornamental both in the garden and in nature, although it is more often a weed. A few species of *Polygonum*, *Eriogonum*, and *Coccoloba* are grown for their exotic properties.

The family is usually considered as the only member of a monotypic order, Polygonales, which is supposedly related to the Caryophyllales (Takhtajan 1959, 1969, Cronquist 1968, Hutchinson 1969), although some authors still place it with the Caryophyllales (Thorne 1968, Benson 1974). Recently, the relationship with the Caryophyllales has been challenged on the basis of pollen data (Nowicke, pers. comm.), and the Polygonales might be better treated as an isolated taxon with no immediate close relatives.

Polygonaceae has been variously divided into subfamilies (Bentham 1856, Bentham & Hooker 1880, Dammer 1892, Roberty & Vautier 1964), and the differences in opinion cannot be resolved here. The one point of near unanimity among all of these authors, and others who have treated the Polygonaceae, is that Eriogonoideae Benth.² is the most distinct subfamily of Polygonaceae and can be readily excluded from the remaining subfamilies. The only serious difference, now largely resolved, has been the relationship of the genus *Koenigia* L. to the western United States genera, *Hollisteria* S. Wats., *Nemacaulis* Nutt., and *Lastarriaea*

Remy in Gay of Eriogoneae Benth., and *Pterostegia* Fisch. & Meyer of the tribe Pterostegeae Torr. & Gray. Bentham and Hooker (1880) proposed that *Koenigia* was related to these genera, placing all of them in a tribe termed Koenigiae. This was directly contrary to Torrey and Gray (1870) who placed *Nemacaulis* and *Lastarriaea* in the tribe Eriogoneae, and *Pterostegia* in Pterostegeae; *Koenigia* was not even mentioned by Torrey and Gray. Roberty and Vautier (1964) removed *Koenigia* from Eriogonoideae, and placed this arctic and subarctic genus in the Polygonoideae where it certainly belongs.

All further comments in this paper will be restricted to the subfamily Eriogonoideae.

GENERIC COMPOSITION OF ERIOGONOIDEAE

The members of Eriogonoideae are restricted to the xeric regions of the New World, with the vast majority of species confined to the western half of central North America from the Tropic of Cancer northward to the fiftieth parallel. In South America, the few species that are known to be native elements in the flora are found in the deserts of northern Chile and scattered parts of adjacent Argentina. The state of California in the United States harbors more species and genera of the subfamily than any other comparable political area; the state also has more endemic genera (five) than any other area. Both *Eriogonum* and *Chorizanthe* have a large number of species in California (about 40 percent of *Eriogonum* and perhaps 70 percent of *Chorizanthe* are in the state), and of all the genera of the subfamily, only two, *Stenogonum* Nutt. and *Harfordia* Greene & Parry, do not occur in California. Three genera occur in both North and South America. *Chorizanthe*

²The authorship of the subfamily name, Eriogonoideae, is here attributed to George Bentham's name "Subordo Eriogoneae" published in deCandolle's *Prodromus* (14: 5. 1856) based upon Article 18 of the present Code (Stafleu et al. 1972), which states "Names intended as names of families, but published with their rank denoted by one of the terms order (*ordo*) or natural order (*ordo naturalis*) instead of family, are treated as having been published as names of families." Unfortunately, in Article 19, which deals with subfamily, no similar provision is stated. For this reason, some may reasonably argue that the correct authorship of the subfamily is Roberty and Vautier (Boissiera 10: 83. 1964).

is strictly an annual group in North America where some 40 of the 50 species of the genus are found, but in South America, all but one (*C. commissuralis* Remy in Gay) of the 10 or so species of the genus are perennials, and no species is common to both continents. The genus *Lastarriaea* is now usually defined to include 2 species (Goodman 1943, Hoover 1966, Munz 1974), *L. chilensis* Remy in Gay of Chile, and *L. coriacea* (Goodman) Hoover of coastal California and northern Baja California, Mexico, although the genus has been considered to be monotypic with two variants (Gross 1913, Goodman 1934) or without any differences (Parry 1884, Abrams 1944, Munz & Keck 1959). The third genus, *Oxytheca* Nutt., has a single species in South America and 8 species are restricted to North America. All of the remaining genera are restricted to North America as are approximately 305 of the 320 species of the subfamily.³

Eriogonoideae is composed of fourteen genera unequally divided into two tribes. The large, typical tribe, Eriogoneae, contains twelve genera and about 318 species, with the majority of the species distributed in two genera, *Eriogonum* (247 species) and *Chorizanthe* (about 50 species). The least advanced member of the tribe is the genus *Eriogonum*. Associated with this genus are a series of small, satellite genera which can trace their probable origin to an extant group within *Eriogonum* as it exists today. Likewise, around *Chorizanthe* are related genera which probably owe their origins to *Chorizanthe*, with *Chorizanthe* itself likely evolved from a now extinct portion of *Eriogonum*. The second tribe, Pterostegaeae, is composed of two monotypic genera which are only superficially related, and whose relationship with Eriogoneae is frankly lost.

Eriogonum is widespread in North America, ranging from east central Alaska (Welsh 1974) southward to central Mexico, and

from the offshore islands of California and Baja California eastward to the Appalachian Mountains of Virginia and West Virginia southward to Florida. In spite of its large size in terms of species numbers, *Eriogonum* has only three generic synonyms. *Eucycla* Nutt. (Nuttall 1848a) and *Pterogonum* H. Gross (1913) are now recognized as subgenera of *Eriogonum* (Reveal 1969a, b; Hess & Reveal 1976), while *Sanmartinia* Buchinger (1950), a name proposed for *Eriogonum divaricatum* Hook. (Reveal & Howell 1976) when it was discovered as an introduction into Argentina (Spegazzini 1902, Moreau & Crespo 1969) and thought to represent a distinct species of *Eriogonum* or a valid genus, is now reduced to synonymy completely.

The genus *Eriogonum* is currently being monographed by myself, but past reviews have been presented by Nuttall (1817), Bentham (1836, 1856), Torrey and Gray (1870), Watson (1877), Stokes (1904, 1936), and Reveal (1969a).

Most closely related to *Eriogonum* is *Oxytheca*. This genus of nine species has been reviewed by those who revised the species of *Eriogonum* (except Nuttall [1817], Bentham [1836], and Reveal [1969a]) at least as far as the genus in North America is concerned, with both Stokes (1904, 1936) and, indirectly, Roberty and Vautier (1964) including the species of *Oxytheca* in *Eriogonum*. Critical reviews of the genus have been presented by Jepson (1913), Abrams (1944), and Munz and Keck (1959) in floristic studies of the California species where seven of the eight North American species are found. Barbara J. Ertter, a graduate student at the University of Maryland, is now monographing the genus. One new species has been discovered from California, and, although recognized as unique by Stokes (1904) and by Goodman (in herbaria annotations), this San Bernardino Mountains endemic has not been described. Two generic

³See note added in proof at end of paper.

segregates have been proposed for species of *Oxytheca*: *Brisegnoa* Remy in Gay (1851), a name actually proposed by Remy prior to 1848 when Nuttall described *Oxytheca*, but whose publication was delayed, and *Acanthoscyphus* Small (1898) for a California species of *Oxytheca*, *O. parishii* Parry, that differs from most species of the genus in having a multiple-awned, nonlobed involucre. *Oxytheca luteola* Parry is now referred to *Goodmania* Reveal & Ertter, and *O. insignis* (Curran) Goodman is placed in *Centrostegia* Gray ex Benth. in DC. (Goodman 1957). In this latter paper, Goodman informally proposed to divide *Oxytheca* into two new genera and at the same time submerge a part of *Oxytheca* in *Eriogonum*. Based upon herbarium annotations, he would have placed *O. dendroidea* Nutt., *O. watsonii* Torr. & Gray, *O. perfoliata* Torr. & Gray, and *O. parishii* in *Eriogonum*, *O. luteola* in a new genus, and referred *O. caryophylloides* Parry, *O. emarginata* Hall, and *O. trilobata* A. Gray to a second new genus. Goodman did not recognize the South American form of *Oxytheca* as a distinct species as proposed by Miers (1851), but retained it as a variant of the North American species, *O. dendroidea* as suggested by Johnston (1929) who proposed var. *tonsiflora* I. M. Johnst. He and Goodman felt the Chilean and Argentinean plants were a distinct form of *O. dendroidea*, which they believed also occurred in other areas of South America. Goodman never published his proposed revision of *Oxytheca*, and Ertter and I are now investigating the genus.

As noted above, one of the species of *Oxytheca* that Goodman proposed to place in a distinct genus was *O. luteola*. This suggestion has recently been accepted by Reveal and Ertter (1976b), who proposed the genus *Goodmania* for this species. *Goodmania* is restricted to alkaline places, dry lake flats, and similar locations in the southern end of the Central Valley of California and elsewhere in the southern part of the state. This monotypic genus seems to be re-

lated to both *Oxytheca* and *Gilmania* Cov.

Somewhat less closely related to *Eriogonum*, but still clearly derived from that genus (rather than *Chorizanthe*), are a series of highly restricted, endemic, western North American genera. *Dedeckera* Reveal & Howell (1976) is a large perennial shrub restricted to a single known location just outside the northwestern edge of the Death Valley National Monument near Eureka Valley in Inyo County, California. This is the only immediate relative of *Eriogonum* that is perennial.

Stenogonum (Nuttall 1848a) is a genus of two species and is restricted to the Colorado Plateau and adjacent regions of Wyoming southward through eastern Utah and adjacent western Colorado into northern Arizona and New Mexico. Until recently, this genus was included in *Eriogonum*, where it had been placed by Hooker (1853) shortly after it was proposed by Nuttall, but it is now considered a valid genus on the basis of its unique involucre construction (Reveal & Howell 1976, Reveal & Ertter 1976a).

Gilmania (Coville 1936), another Death Valley region endemic, was originally proposed under the generic name of *Phyllogonum* Cov. (Coville 1893), but as this name proved to be a later homonym, Coville renamed it for a local Death Valley naturalist, M. French Gilman. Stokes (1904, 1936) maintained the genus as distinct from *Eriogonum*, although Jones (1903) reduced it to *Eriogonum* without comment. Roberty and Vautier (1964) placed *Gilmania* in *Eriogonum* too; but, unlike Jones, who retained the species as distinct, they placed the name in synonymy under *Stenogonum salsuginosum* Nutt. (which they placed in *Eriogonum*), an opinion that is totally incomprehensible.

On the Inner Coast Ranges of California is the monotypic genus *Hollisteria* (Watson 1879). Jones (1908) proposed *Chorizanthe floccosa*, which proved to be a synonym of *H. lanata* S. Wats., but it seems unlikely that Jones comprehended the significance of

his proposal and simply felt the plants represented a species of *Chorizanthe*, and did not consider that he was reducing *Hollisteria* to *Chorizanthe*. Roberty and Vautier (1964) placed the taxon in *Eriogonum*, but this concept has not been followed by anyone, and not even Stokes (1904, 1936) felt compelled to reduce *Hollisteria* to *Eriogonum*, although what her opinion might have been regarding its placement in *Chorizanthe* was never expressed in print.

The genus *Nemacaulis* (Nuttall 1848a, b) is rather widespread in the southwestern United States and extreme northwestern Mexico, with the single species, *N. denudata* Nutt., divided into two weakly defined variants. Stokes (1904, 1936) reduced *Nemacaulis* to *Eriogonum*, perhaps following the ideas of Curran (1885), who noted the close relationship between *N. denudata* and *E. gossypinum* Curran. No one except Roberty and Vautier (1964) has followed this reduction.

A second cluster of genera is related to *Chorizanthe*. Unlike those which have just been reviewed, the satellite genera in this section can be traced to extant sections of *Chorizanthe*.

Chorizanthe itself is a genus of perhaps 50 species, with about 40 species found in west-central North America, and the remaining 10 or so restricted to northern Chile in South America. All of the species in North America are annuals, while all but one of the South American species are subfruticose perennials. The genus has been monographed only by Bentham (1836, 1856), although the North American species have been revised by Torrey and Gray (1870), Watson (1877), Parry (1884), and Goodman (1934). Remy (1851) and Philipp (1864, 1873, 1895) have added species to the South American component of *Chorizanthe*.

Like *Eriogonum*, the generic concept of *Chorizanthe* has changed over the years, with *Chorizanthe* being defined in both a broad and a strict sense. As the genus is outlined here—and it is done so only in a

tentative fashion—a middle-of-the-road approach is proposed. Several segregate genera have been proposed from members frequently placed in *Chorizanthe*. These genera are *Mucronea* Benth., *Lastarriaea*, *Centrostegia*, *Acanthogonum* Torr., and *Eriogonella* Goodman. In the following treatment, *Mucronea*, *Lastarriaea*, and *Centrostegia* are recognized as distinct from *Chorizanthe*, with *Acanthogonum* and *Eriogonella* retained in *Chorizanthe*.

The genus *Mucronea* (Bentham 1836) was described at the same time that *Chorizanthe* was proposed, and it was retained as a distinct genus by Bentham (1856) in his monograph on Eriogonoideae in deCandolle's *Prodromus*. Torrey and Gray (1870) reduced *Mucronea* to *Chorizanthe*, and their opinion was followed by Bentham and Hooker (1880) a decade later. Goodman (1934) reintroduced *Mucronea* into the literature when he distinguished it from *Chorizanthe* in his monograph on the latter genus. However, even with Goodman's study, the genus remained suppressed (Abrams 1944, Munz & Keck 1959) except for Hoover (1970), who recognized the genus in a local flora. As defined here, the genus is considered to have two species, both of which are restricted to California.

Lastarriaea was proposed by Remy in Gay's *Flora Chilena* (1851), but it was not associated with the tribe Eriogoneae (Bentham 1856) until Torrey and Gray (1870) placed the genus in the tribe. Bentham and Hooker (1880) removed it, *Hollisteria*, and *Nemacaulis*, along with *Pterostegia*, and placed them in the tribe Koenigeae. Except for Dammer (1892), this significant departure has not been followed to any degree.

As now defined, *Lastarriaea* contains two species, one in North America and one in South America (Goodman 1943, Hoover 1966).

The genus *Centrostegia* was published for Asa Gray by Bentham (1856) and considered at the time to be a monotypic genus. In 1870, Torrey and Gray added a second species, but in 1877, Watson reduced the

genus to *Chorizanthe*, where it remained until Goodman's revision of *Chorizanthe* in 1934. In 1957, Goodman revised *Centrostegia*, bringing the number of species in the genus to four. One species, *Centrostegia insignis* (Curran) A. A. Heller (1910), was originally described as a species of *Chorizanthe* by Curran (1885) but placed in *Oxytheca* by Goodman (1934) without comment. In short, this single, unusual species has been batted around in three separate genera, and it still seems out of place in *Centrostegia*. As now defined, *Centrostegia* occurs from Arizona and Utah westward to California, where it is found from Monterey and San Luis Obispo counties southward.

Of these three genera, all of which have at one time or another been associated with *Chorizanthe*, data would now seem to indicate that only *Mucronea* is actually all that close to *Chorizanthe*, with *Centrostegia* occupying a position somewhat intermediate between *Eriogonum* (not *Oxytheca*) and *Chorizanthe*, and *Lastarriaea* well isolated from all of the genera but still closer to the *Chorizanthe* complex than the *Eriogonum* complex.

Preliminary studies on the *Chorizanthe* complex have revealed some major areas of investigation for future studies. The most important one is to determine the relationship between the northern annuals and the southern perennials in the genus *Chorizanthe*. The type of the genus is a South American perennial, *C. virgata* Benth., and these perennials differ markedly from the annuals. Current plans call for a detailed study of the South American species, which have not been revised in over 100 years. It is hoped this group of plants will be the subject of a doctoral dissertation. A second area of investigation is whether or not the genus *Acanthogonum* should be recognized and, if so, what members of *Chorizanthe* should be placed in it.

All of the genera discussed to this point belong to the tribe Eriogoneae. The second tribe of the subfamily is Pterostegaeae. This taxon may be characterized by the bisaccate

bracts which become enlarged, scarious, and reticulate in fruit, and the consistently opposite leaves.

The genus *Pterostegia* is a monotypic genus of low, spreading to decumbent annual herbs. Described by Fischer and Meyer (1835) from material gathered by the Russian explorers near Fort Ross in California, the genus can be rapidly distinguished from all other members of Polygonaceae by its floral features and fruiting characteristics. A major problem has been how to interpret the bisaccate bracts. Fischer and Meyer completely misunderstood the relationship of the bracts of *Pterostegia* as they attempted to relate these bracts to those of *Eriogonum*. Bentham (1856) misunderstood the bracts too, attempting to define them as three leaves with a contiguous margin which are expanded into a dorsal wing or crest. Torrey and Gray (1870) stated that the bracts were homologous with the bracts of *Nemacaulis*, but even this seems most unlikely today, although the concept expressed by them was accepted by Bentham and Hooker (1880). The involuclral bracts of *Pterostegia* are two-lobed, enlarged in fruit, and are simply unlike anything found in any genus of Eriogoneae.

Pterostegia is a rather variable species which ranges from Oregon southward to northern Baja California and eastward into Utah and Arizona. It does not seem to be divisible into infraspecific elements although Nuttall (1848a) suggested some segregates.

The second genus of Pterostegaeae, *Harfordia*, was proposed by Greene and Parry in a paper published by Parry (1886). The year before, Greene (1885) had described *Pterostegia galioides* Greene, and, while he placed the species in *Pterostegia*, it was the first time that good specimens of *P. macroptera* Benth. (Bentham 1844) were found. Bentham's descriptions of his species, published both in 1844 and 1856, lacked the fine detail, and he was not even sure whether the plants were annuals or perennials. It is likely that the lack of adequate material accounted for the long delay in as-

certaining the significant differences between the type species of *Pterostegia*, *P. drymarioides* Fisch. & Mey., and *P. macroptera*. Once *Harfordia* was described, it was immediately accepted, and the genus is now well recognized (Shreves & Wiggins 1964). At present, *H. macroptera* (Benth.) Greene & Parry is known only from the west coast of central Baja California, Mexico.

ORIGIN OF ERIOGONOIDEAE

The origin of Eriogonoideae is unknown. The subfamily is clearly a member of Polygonaceae, for it shares with the other subfamilies of the family a large number of morphological and biochemical similarities, and the subfamily Eriogonoideae cannot be raised to the familial level as proposed by Meisner (1841) without violence to our understanding of families in the Magnoliophyta. Eriogonoideae has a single, basal, bitegmic, crassinucellate ovule similar to that of *Polygonum* and has the typical trinucleate pollen of the family. Still, these are features which are not only typical of Polygonaceae, but of Plumbaginaceae and nearly all of the families commonly associated with the Caryophyllales (Cronquist 1968). Eriogonoideae also shares with the other subfamilies of Polygonaceae the copiously laden endospermous seeds and the anthocyanins pigmentation. The subfamily does differ from the other subfamilies in lacking the distinctly sheathing stipular ochrea of the leaves (although an ochrea is weakly present in some perennial species of *Chorizanthe*), and the pollen of the subfamily is the least specialized of all subfamilies of Polygonaceae (Nowicke, pers. comm.) suggesting that, as a group, Eriogonoideae may be a rather primitive member of Polygonaceae. Equally important in this regard, it may also mean that Eriogonoideae, as a group, has retained many of the least specialized features of the family due to a lack of modification in organs which have occurred in other taxa.

Although the critical similarities between

the subfamilies certainly associate these taxa of Polygonaceae into a distinct family, the place and mode of development of Eriogonoideae from the rest of Polygonaceae is now obscured by time and compounded by a lack of a fossil record. No one group of genera outside of the Eriogonoideae can be considered the exact point of origin of the subfamily, and for this reason, the subfamily (or tribe) has long been considered unique within Polygonaceae (Bentham 1836, Goodman 1934, Roberty & Vautier 1964). Based on preliminary pollen data from extant taxa now available from the work of Dr. Joan Nowicke at the Smithsonian Institution, it seems clear that Eriogonoideae is clearly differentiated from all but the South American tropical genus *Triplaris* Loebl. This is the only genus which has a similar, unspecialized pollen grain (and thus different even from the related American tropical genus *Ruprechtia* C. A. Meyer), but based on extant data on chromosome numbers, gross morphology, and other anatomical and morphological features (especially in the inflorescence), it seems most unlikely that the tribe Triplarieae C. A. Meyer and the subfamily Eriogonoideae have been connected in any but the most remote fashion.

Roberty and Vautier (1964) placed Triplarieae in the subfamily Calligonoideae Roberty & Vautier which they defined as a group of New and Old World genera. Dammer (1892) referred the tribe to Coccoloboideae Dammer, a basically shrubby or arborescent taxon about equally divided in the New and Old World. Dammer's suggestion seems more reasonable as he defined the Coccoloboideae to include (using current nomenclature) such genera as *Coccoloba*, *Muehlenbeckia* Meisner, and *Triplaris*—all genera with ruminated endosperm. Unfortunately, all genera of Eriogonoideae have a smooth endosperm. Meisner (1856), Bentham and Hooker (1880), and Dammer (1892) all placed Eriogonoideae in a position in their revisions of the Polygonaceae which would imply that Eriogonoideae is the least specialized of the family. Roberty

and Vautier placed the subfamily at the end of their treatment; most certainly Roberty and Vautier are correct in their assessment of the placement of the subfamily in the family, for Eriogonoideae is the most advanced member of the extant subfamilies of Polygonaceae and not the least specialized. In Meisner, Bentham and Hooker, and Dammer, interestingly, the Triplarideae was considered the most advanced member of the subfamily Polygonoideae (Meisner and Bentham and Hooker) or Coccoloboideae (Dammer). If this is indeed the case, then it logically can follow that a possible origin of the Eriogonoideae may have been within an ancient taxon that, by definition, might include the basic expression from which the Triplarideae has evolved or in fact was a part. At no time, however, has *Triplaris* or *Ruprechtia* played a direct role in the origin of any genus within Eriogonoideae.

It is likely that the divergency of Eriogonoideae from the rest of Polygonaceae has been so fundamental, so sudden, and so successful, that the new subfamily has completely swamped those groups (or that group) from which it arose. If this divergency is an ancient one, as I suggested some years ago (Reveal 1969b), and occurred at the beginning or slightly before the start of the Tertiary some 65 million years ago, then the loss of such intermediate stages of evolutionary development is to be expected. However, if the origin of the subfamily has been well within the Tertiary, as now seems much more likely, then the loss of the intermediate forms is a matter of the explosive success and highly competitive nature of the new form (in this case, the earliest members of Eriogonoideae) as opposed to the rather static parental type (see Stebbins [1974] for a detailed discussion of this type of explosive evolution above the generic level).

As just noted, it now seems more reasonable to assume that Eriogonoideae arose during the Tertiary, and probably during the Oligocene or Miocene epochs (7 to 38 million years ago) when there was a general

drying of the climate coupled with the rapid development and increase of herbaceous angiosperms (Gray 1964, Axelrod 1966, Tidwell et al. 1972). Pollen grains, attributable to *Eriogonum*, have been found in the Quaternary, which began some 7 million years ago (Leopold, pers. comm.). If this assumption is correct, then perhaps the subfamily Eriogonoideae had its origin from a subtropical group of New World polygonaceous plants near the beginning of the drying period during the Oligocene, which split off into a tropical complex (something like *Triplaris*) and a northern temperate complex (something like *Eriogonum*). This point of origin has subsequently been lost, with the extinct relatives of *Triplaris* and *Eriogonum* extending and amplifying the differences between the two extremes to a point that now only the mere hint of relationship may be noted in a conservative feature such as pollen morphology. If the theories of Takhtajan (1969) and Stebbins (1974) are correct regarding the differential rates of specialization between tropical and xeric temperate groups, then one may assume that the relatives leading to *Triplaris* have undergone less specialization and differentiation than the relatives leading to *Eriogonum*. This would seem to be the case here, especially when one looks at the reduction of the inflorescence in *Eriogonum* to a cluster of flowers, the reduced stature of *Eriogonum*, and the great proliferation of species in the Eriogonoideae when compared with the Triplarideae.

Over the years I have vainly searched the temperate members of Polygonaceae, and especially those of Asia, for a hint to the origin of *Eriogonum*. None has been found. Stebbins (1974) has cautioned us to realize that in evolutionary events such as the origin of taxa above the species rank extinction and extensive changes in the distribution and ecology of a taxon may occur which can substantially change one's outlook as to the possible site and point of origin for a given group. It now seems reasonable to look to the New World tropics for a

point of origin rather than the Old World steppes. Certainly, the pollen data just recently reported to me by Nowicke has greatly strengthened this preconceived idea. The origins of the Eriogonoideae very likely have revolved around the reduction of the inflorescence from an extended one (such as in *Ruprechtia* or *Triplaris*) to a capitate one, the development of an involucre due to the fusion of subtending bracts on the inflorescence, and the reduction of stature from a shrub or small tree to a subshrub or low shrub. The final step, of course, has been the development of an ability to evolve successfully in a xeric habitat rather than in a mesic, subtropical, or tropical habitat. To my knowledge, none of these steps is extant today.

It was proposed by me (Reveal 1969b) that the probable ecological place of origin for *Eriogonum* was in a xeric site, and that the first forms of the genus were subshrubs or low shrubs. This suggestion has been seconded by Stebbins (1974), and there seems to be little reason to alter this opinion. It is important to note that this statement relates to one genus, *Eriogonum*, and not to the origin of the subfamily. It seems to me that the stages of development leading from the tropical origin of the precursors of the Eriogonoideae to the extant genus *Eriogonum* must have taken many different directions, a great deal of time, and undergone many different attempts before arriving at this modern genus. It is now impossible to close that gap, since the history of the Eriogonoideae during the Tertiary is unknown.

The most generalized form of *Eriogonum* that exists today is a low, rounded shrub with cauline leaves, cymose inflorescences, small smooth achenes, and an unspecialized flower with monomorphic tepals. These shrubs occur in xeric habitats mainly in the pinyon-juniper woodlands of the Great Basin in Utah and Nevada. Even so, these species of *Eriogonum* are highly specialized as all are tetraploids, and no diploid species are known to exist in the genus (Stebbins

1942, Stokes & Stebbins 1955, Reveal 1969b). Therefore, *Eriogonum*, as it exists today, is a highly evolved group, and no species now exists which could point to the initial element(s) which might have evolved from other, more primitive, subtropical taxa of Polygonaceae.

The assumption that *Eriogonum* is the most basic genus of the subfamily seems reasonable on the basis of morphological considerations, especially in the makeup of the inflorescence and involucre. However, I suspect, that the most ancient extant members of the subfamily are the perennial species of *Chorizanthe*. As shall be discussed below, *Chorizanthe* likely evolved from *Eriogonum*, and not the other way around. However, one feature found in these perennial species of *Chorizanthe* seems to hint at their ancientness: they have what can only be considered as weakly defined, fibrous remains of ochrea. If these species of *Chorizanthe* should prove to be diploids, this would reinforce their evolutionary significance. Based upon an examination of the gross morphology of these plants, one must add to the definition of the earliest members of Eriogonoideae the presence of an ochrea.

If the genus *Eriogonum* underwent its early development in a xeric habitat dominated by pinyon-juniper woodlands, then where was such a site in the Miocene or early Pliocene epochs when the genus was undergoing its earliest development?

During the Miocene, the Great Basin was dominated by extensive coniferous forest, with the Sierra Nevada to the west about 1000 m in altitude, and thus an ineffective rainshadow (King 1959). It is important to note that these coniferous forests were temperate in nature, with the subtropical forests of the Oligocene largely pushed to the south. Axelrod (1950) has suggested the existence of two major geofloras, with the Arcto-Tertiary geoflora of hardwood-deciduous and conifer forests dominating the Great Basin region, and the Madro-Tertiary geoflora of small-leaved, drought-resistant

shrubs and trees of the southwestern United States and northwestern Mexico. Axelrod (1958) states that the Madro-Tertiary geoflora moved northward into the Great Basin in Early Pliocene, but did not entirely replace the Arcto-Tertiary geoflora.

It would seem possible that *Eriogonum* may have undergone its early development and differentiation in the Madro-Tertiary geoflora during the Miocene and became well established in the Arcto-Tertiary geoflora in at least two different expressions: one typified by the subgenus *Eucycla* (Nutt.) Kuntze in Post & Kuntze (with such species similar to *E. microthecum* Nutt. or *E. corymbosum* Benth. in DC.) and the other of members typical of the subgenus *Oligogonum* Nutt. (with such species similar to *E. umbellatum* Torr. or *E. flavum* Nutt. in Fras.). Out of the Madro-Tertiary geoflora possibly came such subgenera as *Eriogonum* and *Pterogonum* (H. Gross) Reveal which contain such species as *E. longifolium* Nutt., *E. atrorubens* Engelm. in Wisliz., and *E. alatum* Torr. in Sitgr., or their progenitors (Hess & Reveal 1976). Nonetheless, the basic expression of the genus would have belonged to the subgenus *Eucycla*, which is basically a taxon of xeric, pygmy coniferous forests. It is also likely that *Chorizanthe* evolved during this period of time from the subgenus *Eucycla*, probably when the subgenus was in the Madro-Tertiary geoflora and before the subgenus underwent its modern-day development of species complexes now typically found in the Great Basin.

EVOLUTION WITHIN ERIOGONOIDEAE

If the hypothesis is correct that *Eriogonum* is the most primitive extant member of the subfamily Eriogonoideae, then a number of corollaries may be presented.

Within *Eriogonum* itself, if the basic expression of the genus was a low, spreading subshrub or shrub with alternate leaves, cymose inflorescences, and unspecialized tepals, then the subgenus *Eucycla* was the initial expression within the genus. As just

noted at the end of the previous section, it is probable that the differentiation of the subgenera *Eucycla*, *Eriogonum*, *Oligogonum*, and *Pterogonum* occurred during the Late Miocene or Early Pliocene in the Madro-Tertiary geoflora of northern Mexico and the southwestern United States. Three of these subgenera of *Eriogonum* are fairly distinct from one another, with no inter-connecting forms. It is felt that while *Eriogonum* and *Pterogonum* evolved from *Eucycla*, these two did not evolve from any extant member of *Eucycla*. As for *Oligogonum*, it is close to *Eriogonum* and more distantly related to *Eucycla*, and thus both *Oligogonum* and *Eriogonum* may have developed from extinct, primitive members of *Eucycla* at approximately the same time. Of the remaining subgenera, *Clastomyelon* Cov. & Morton, *Micrantha* (Benth.) Reveal, *Ganysma* (S. Wats.) Greene, and *Oregonium* (S. Wats.) Greene, all can be traced rather directly to the subgenus *Eucycla* without any major difficulties.

As for *Eucycla*, it has developed every perennial habit expression of the genus *Eriogonum* but one, the monocarpic habit of *E. alatum* of the subgenus *Pterogonum*. The subshrub or low shrub habit is widely seen in the less specialized members of *Eucycla*. Such plants are typically seen in the pinyon-juniper (or pygmy) woodlands throughout the western part of central North America today, or essentially the entire geographical range of the subgenus which extends from the fiftieth parallel southward to the Tropic of Cancer. Also found in the pygmy woodland zone are several different kinds of herbaceous perennial expressions belonging to *Eucycla*. Unlike the shrubs which tend to be species of widespread distribution, the herbaceous perennials tend to be more restricted in their range. Some of these species evolved within the zone and have remained while others have extended themselves beyond the confines of the zone, and still others, in more recent evolutionary times, have entered the zone from other areas. From the pygmy

woodland zone, species of *Eriogonum* have migrated into dry, xeric clay habitats, into grasslands or chaparral habitats, and into alpine zones and off-shore islands. In all cases, the present members of the subgenus are tetraploid, derived species, and while the majority of morphological expressions are found in the pinyon-juniper belt, the majority of explosive evolution within *Eriogonum*, and in all of its related genera (except for the most initial phases of *Chorizanthe*), owe their origins to their survival in ecological life zones other than the pygmy woodlands.

The origins of both of the predominantly annual subgenera, *Ganysma* and *Oregonium*, probably owe their origins to the subgenus *Eucycla* and probably had an initial differentiation in the pinyon-juniper woodlands of the West. Once again the basic expression of these subgenera are generally widespread and found mainly in this habitat. However, unlike portions of *Eucycla*, it seems—especially in *Ganysma*—that much of the initial evolutionary development of these subgenera have been lost over time, because there are widely scattered species of *Ganysma* in other habitats in which the species are obviously primitive but by no means ancient.

The temperate arid regions of the inland portions of North America exhibit the unique combination of selective drought and cold temperatures, conditions which have likely played a major role in the evolution of the shrubby habit from which herbaceous and caespitose perennial species could have evolved (Axelrod 1966). The shrubby and subshrubby species of *Eriogonum* and *Chorizanthe* have certainly been subjected to the selective pressures of seasonal cold, coupled with enough summer moisture to sustain growth, and the ability to occupy habitats that are protected enough to allow for long-term survival in extended periods of stress. By looking at a pygmy woodlands as the original home of *Eriogonum* and its first major dichotomy, *Chorizanthe*, one can understand the variety

of habit and morphological expression in this ecological habitat, and the economy in terms of species diversity in this zone. On the whole, the explosive evolution of the modern-day species of *Eriogonum* and its related genera, and *Chorizanthe* and its related genera, has been areas in of extreme environmental stress outside the protective (such as they are) confines of the pinyon-juniper belt. Without a doubt, the majority of the genera related to *Eriogonum* owe their origin to their successful adaptation to a stress condition, mostly selective drought, accompanied by the occupation of ecological areas on the margins of protective life zones. However, as we shall see, the subgenus *Eucycla* has given rise only to the other subgenera of *Eriogonum*, *Chorizanthe*, and *Dedeckera*, but none of the other genera. *Oxytheca*, *Stenogonum*, *Gilmania*, *Goodmania*, *Nemacaulis*, and perhaps *Hollisteria* owe origin to *Eriogonum* subgenus *Ganysma*, while *Mucronea*, *Centrostegia*, and perhaps *Lastarrianea* owe their origin to annual species complexes of *Chorizanthe*. And note, all of these genera (except the primitive members of *Chorizanthe*) are basically taxa of areas of extreme aridity, and basically adapted to the annual habit (all but *Dedeckera*).

The one major adaptation which distinguishes *Chorizanthe* from *Eriogonum* is a combination of the production of an awned involucre and the reduction in the number of flowers per involucre. I believe the production of an awned involucre has occurred several times in the history of the subfamily, much as the total loss or reduction of an involucre has occurred several different times and places in the taxon.

The key to understanding the origin and evolution of *Chorizanthe* lies in the unstudied South American perennial species. An examination of available herbarium material seems to point the origin of these perennials to the subgenus *Eucycla* of *Eriogonum*, a theory which seems reasonable if *Eriogonum* is, as I suspect, the basic element of the subfamily. There are, however, some diffi-

culties which in theory can be excused but need to be mentioned.

If *Chorizanthe* evolved from *Eriogonum* subgenus *Eucycla*, it did not evolve from any extant group of the subgenus. One can account for the subshrubby habit of the perennial *Chorizanthe* as having come from *Eucycla*. Even the hooked, awned condition of the involucre could be traced to the subgenus as several extant species of *Eucycla* have long, sharply acute involucre lobes which, while not awned, could point to a stage in the development of the awned condition. The narrow, essentially basal leaves of *Chorizanthe* can be traced to *Eucycla*, as can the congested, cymose inflorescence. Two major drawbacks exist. One is the straight embryo of *Chorizanthe* (Goodman 1934), whereas all species of *Eucycla* have a curved embryo (Reveal 1969a, b). The second is the six-lobed involucre of *Chorizanthe*, while the majority of species in *Eucycla* are five-lobed.

The critical hint here, I believe, is the presence of the remains of the ochrea in some species of South American *Chorizanthe*. As Grant (1971) has noted, a given character may or may not be selected for or against, and thus, while the direction of the subfamily Eriogonoideae has been to get rid of the ochrea, at sometime in its history of divergency from the rest of Polygonaceae it must have possessed this feature. If, as I suspect, the perennial species of *Chorizanthe* are the most ancient extant members of the subfamily, then it would follow that these plants would exhibit some of the more primitive features of the subfamily and provide helpful keys to its origin. By the same token, while I accept *Eriogonum* as the basic expression of the subfamily, and *Chorizanthe* as a derived element, one need not look further than extant and derived members of *Eriogonum* to find all unique features of the South American perennials except the ochrea. Thus, if *Chorizanthe* evolved as a preliminary expression from *Eucycla*, as did the subgenera *Eriogonum* or *Oligogonum*, then suddenly we find species

of *Eriogonum* with a straight embryo and a six-lobed involucre. The genus *Oxytheca*, which can trace its immediate origin to *Eriogonum* subgenus *Ganysma*, has awned involucres, and the reduction in the number of flowers per involucre can be seen in several different groups of *Eriogonum*, although admittedly this feature is almost entirely restricted to annual species.

The next critical step in this discussion is how did the perennial members of *Chorizanthe* get to South America while *Eriogonum* did not, and if *Chorizanthe* evolved from *Eriogonum* subgenus *Eucycla* in North America, why are there no perennial species of *Chorizanthe* in North America?

The first part of this question can be easily answered. The only members of Eriogonoideae in South America are those which have a distinctly awned, or hooked, involucre lobe. As Stebbins (1974) has pointed out, such an adaptation can be a successful means of long-distance dispersal. Thus *Eriogonum* (with the exception of *E. divaricatum*, an annual species which was found as a waif in eastern Argentina) is perhaps lacking from South America due to the absence of an awned involucre. The second part of this question, why the perennial species of *Chorizanthe* are missing from North America, is much more difficult.

Two options exist about the existence of perennials in South America and their lack in North America, and a third option can be proposed on the basis of either of the first two options if future studies should make such an option necessary from a taxonomic point-of-view.

The first two options are closely intertwined and deal with the actual origin of the perennial species in South America and the annual species in North America. Assuming the idea that *Chorizanthe* evolved as a perennial group from *Eriogonum* in North America, then it had to have migrated to South America as a perennial and become established as a perennial. The South American populations, I believe, have remained essentially unchanged since their (or its) in-

ital introduction with some speciation occurring there within rather limited parameters. One hint that this is so is that all of the perennial *Chorizanthe* species fall within extremely narrow limits morphologically, and, while several species (close to 25) have been described, the actual number of valid species seems to be much less than that. The one annual species in South America is apparently a much more recent introduction than the perennial species because it is closely related to the single most widespread annual species in North America (Goodman 1934).

The first option states that *Chorizanthe* evolved in North America and migrated as a perennial to South America as a single introduction, with the North American perennials gradually being replaced by annual species. In South America, the perennial species were subjected to little direct selection pressure, while in North America the perennial members of *Chorizanthe* were subject to intense pressures from the rapidly evolving and highly competitive, closely related genus *Eriogonum*. In order to survive and compete against *Eriogonum*, which, I feel, was rapidly adopting the annual habit, *Chorizanthe* also had to change if this hypothesis is feasible.

The second option is that the perennial species of *Chorizanthe* in North America became extinct, while the South American species remained. The annual habit then developed in Chile, and only the annual species were introduced into North America. Raven (1963) has noted that, while the majority of species probably migrated north to south, some certainly went from south to north. Once in North America, the annual species underwent active adaptive radiation similar to that observed in such annual groups of *Eriogonum* as the subgenera *Ganysma* and *Oregonium*.

The third option states that the South American perennials represent a genus of plants distinct from the North American (and one South American) annuals. If this is so, then the name *Chorizanthe* would be ap-

plied to the South American perennials, while the annual species would be called *Acanthogonum*, or, if that genus proves distinct, *Eriogonella*. This option takes on added significance if the following scenario should prove correct after careful systematic studies. If indeed *Chorizanthe* evolved as a perennial and migrated southward, and the northern element became extinct, did the annual species evolve prior to the extinction of the perennial group or did the annual species begin from a whole new series of events? In option one, I have accepted the first part of this question, but if the second were the case, then it will be impossible to retain the North American annuals in the genus *Chorizanthe*.

The recently discovered *Dedeckera eurekaensis* probably evolved from the subgenus *Eucycla* of *Eriogonum*, and most likely from the section *Corymbosa*. Its origin is likely most recent. It differs from all other members of the subfamily in having a head of subsessile or sessile flowers, borne on a slender peduncle and subtended by two to five foliaceous bracts, and a single, short-pedicellate axillary flower at the base of each peduncle. It differs from *Eriogonum* in lacking an involucre tube. This monotypic genus is known only from a single site where about 200 individual plants are found. It is likely that the genus evolved in place within recent history and, while its range has expanded and decreased throughout its brief history, it is unlikely that the plant has been beyond the restrictive ecological confines of the Death Valley region of eastern California.

The pubescence of *Dedeckera* is similar to that of *Eriogonum intrafractum* Cov. & Morton, another Death Valley endemic, which is the only representative of the subgenus *Clastomyelon* and a few other members of *Eriogonum*. Of all the subgenera of *Eriogonum*, *Clastomyelon* is the most distinctive on pure morphological grounds in that the stems are broken into a series of ringlike segments, the numerous flowers rupture the involucre tube into irregular

segments, and the bractlets are foliaceous at least in part. While it is possible to trace the origin of *E. intrafractum* to the subgenus *Eucycla*, where *D. eurekensis* also evolved from, both are amazingly distinct, with *D. eurekensis* significantly more so than *E. intrafractum*. It is interesting that in the Death Valley area, where speciation has been rather spectacular (Stebbins & Major 1965), Polygonaceae should be blessed with so many different expressions. Much like *Gilmanina*, which will be discussed below, *Dedeckera* and *E. intrafractum* have come about in recent times, influenced by the environmentally profound selection pressures of the area.

The remaining satellite genera related to *Eriogonum* evolved from the subgenus *Ganysma*.

Oxytheca is being studied currently by Ertter and me to determine the exact make-up of this genus. We have excluded *O. luteola*, placing it in a new genus, *Goodmania*. The remaining nine species, however, may or may not be all related. *Oxytheca dendroidea*, *O. watsonii*, and the South American plants are related to *Eriogonum spergulinum* A. Gray, and, based on this close morphological similarity, Goodman (in herbaria) has placed these plants in *Eriogonum*. *Oxytheca perfoliata* probably belongs to this complex of species (Goodman would have placed the taxon in *Eriogonum*), but it is morphologically distant from the other members. As for *O. parishii* and an undescribed taxon from the San Bernardino Mountains of California, they present a problem. Goodman (in herbaria) would have placed these in *Eriogonum*, but both seem more closely related to *E. apiculatum* S. Wats. and *E. parishii* S. Wats. than *E. spergulinum*. Small (1898) placed *O. parishii* in a monotypic genus, *Acanthoscyphus*. It is possible that *Acanthoscyphus* should be recognized if it can be shown that *O. parishii* and its related taxon are distinct from that group of *Oxytheca* species typified by *O. dendroidea*.

This complex of species (excluding the

Oxytheca parishii complex for a moment) seems to have developed in the pygmy woodlands of the Great Basin and, in particular, along the western edge of the Great Basin. This is a complex of volcanic sandy soils that are widely scattered. I suspect the group evolved during the Quaternary (probably the Pleistocene), with the introduction of the South American phase in recent geological time (see Raven 1963).

Goodman (in herbaria) placed *Oxytheca caryophylloides*, *O. emarginata*, and *O. trilobata* in a new genus. Our preliminary studies of these species seem to indicate that they too developed from *Eriogonum apiculatum*, *E. parishii* complex, and perhaps one should consider if these species too ought not to be referred to *Acanthoscyphus*. These three species differ from *O. parishii* and its undescribed relative in having a five-lobed involucre instead of the nonlobed tube with 4 to 30 long bristled awns. All of these plants are found in the granitic mountains of southern California and northern Baja California and occur in approximately the same type of ecological niche.

I have come to look upon *Oxytheca parishii*, *O. caryophylloides*, *O. emarginata*, and *O. trilobata* as a group that has evolved in the Pleistocene in the mountainous region of southern California and adjacent Mexico as the result of sudden and explosive evolutionary changes in the gene makeup of the rapidly developing annual species of both *Eriogonum* and *Chorizanthe*. This is not to say that *Chorizanthe* played a direct role in the development of these species, but one should remember that *Centrostegia* (and in particular *C. insignis*) probably developed at the same time, and this genus is similar to *Chorizanthe*. Thus, I suspect, a whole series of rapid changes were in the process at this time in a small portion of *Eriogonum*, which possibly resulted in this group of *Oxytheca*, *Centrostegia*, and perhaps (if option three is correct) the annual species of *Chorizanthe* as well. If this conclusion should prove correct with regards to the species now placed in *Oxytheca*, then Good-

man would have been proved correct, and these species would have to be placed in a different genus.

Stenogonum is a step-child in this group of satellite genera. It is closely related to *Eriogonum*, differing mainly in the construction of the involucre bracts. While in *Eriogonum* the involucre is distinctly tubular, the involucre of *Stenogonum* is composed of two whorls of three lobes. That this condition is possible within a genus clearly and closely related to *Eriogonum* is an important step, because it does demonstrate the potential for a six-lobed or three-lobed involucre as found in the annual species of *Chorizanthe*.

Stenogonum evolved from the *Eriogonum inflatum* Torr. & Frém. complex of the subgenus *Ganysma*. It is thought that the origin of this clay-inhabiting genus is relatively recent and has evolved to a point about on the par with the degree of divergence seen in *Oxytheca*. *Stenogonum* is an annual which has evolved from a "hot desert" complex on the Colorado Plateau, which is an area somewhat intermediate between the Mojave Desert and the Great Basin in terms of physiological stress. *Eriogonum inflatum* var. *inflatum* is found on the Plateau, but the more common phase is not the perennial var. *inflatum*, but the annual var. *fusiforme* (Small) Reveal. Likewise, var. *inflatum* is usually found in rocky places above the clay hills and flats, while var. *fusiforme* is typical of the clay sites. Thus it is that the genus *Stenogonum* has evolved by successfully occupying the clay habitat that, for the most part, members of the *E. inflatum* complex cannot enter.

Two genera are difficult to directly associate with *Eriogonum*, and both perhaps have recently evolved in the subfamily. They are *Goodmania* and *Gilmania*. The two seem to be related, as both are prostrate to low-spreading annuals with pubescent yellow flowers, cauline leaves, and small, smooth achenes. *Goodmania* has involucre bracts which subtend each cluster of flowers and act as a protective involucre.

In *Gilmania*, all involucre bracts are lacking, but the three foliaceous leaves, when the plants are immature (but that particular branch is in full flower), are held close together by the shortened internodes so that each cluster of flowers is positioned above the lower whorl of three leaves so that the flowers are protected both by these leaves and the whorl of upper leaves as well. In this condition, the long pedicels extend the ripened flowers beyond the protective confines of the three leaves so that pollination may occur. In this fashion, the flowers of *Gilmania* are better protected from the elements than those of *Goodmania*.

Goodmania could possibly be traced to *Oxytheca*, but I think not. True, it has an awned involucre bract, but, in fact, these bracts are just that and they are not arranged into a distinct tube. The individual bracts can be separated from each other without disruption of tissue on an adjacent bract. There is one bract that is longer than the other four bracts which is unlike any species of *Oxytheca*, but is a condition that is seen in some species of annual *Chorizanthe*. The flowers of *G. luteola* are yellow, and no species of *Oxytheca* has yellow flowers, and the plants of this species are glabrous and bright green while those of *Oxytheca* are glandular (at least in part) and usually reddish or grayish in color. As I look about the subfamily, I see a possible close relationship with the subgenus *Oregonium* for this genus and *Gilmania*, and in particular *Eriogonum divaricatum*. The subgenus *Oregonium* underwent a major upheaval in the hot, dry foothills of western California, but *E. divaricatum*, *E. puberulum* S. Wats., and other similar species are more typical of the Great Basin. Thus, while this group of species of *Eriogonum* may hint as a possible place of origin for *Goodmania* and *Gilmania*, the group seems unsatisfactory, and no extant subfamily of *Eriogonum* really reveals a logical place of their origin.

As noted above, these two genera seem to be recently evolved genera. *Goodmania* is

usually found on the plains of old dry lake beds in areas which were covered by water during recent glacial periods. *Gilmania* occurs on the lower rim of Death Valley on alkaline soils near sea level, and thus in areas that were covered by water less than 50,000 years ago. It is likely, therefore, that both genera underwent their evolutionary development at approximately the same time, taking advantage of the same type of opening environment niche.

The origin of *Gilmania* is somewhat more difficult to postulate than that of *Goodmania*. Cauline leaves in *Eriogonum* annuals are infrequent, and when present are rarely arranged in a pattern similar to that of *Gilmania*, nor are they like the leaves of *Goodmania*. In *Goodmania* the leaves are two and opposite, varying from laminar at the lower nodes to acicular at the upper nodes. In *Gilmania*, the leaves are in threes, with two of the leaves opposite, and the third opposite the next branch; all of the blades are laminar. It seems unlikely that both *Gilmania* and *Goodmania* evolved from precisely the same element within *Eriogonum*, but they probably did arise within the same subgenus. I strongly suspect that the selective evolutionary pressures have been much greater on *Gilmania* than *Goodmania*, thus accounting for the great degree of demarcation of *Gilmania*.

Curran (1885) was the first to call attention to the close relationship between *Eriogonum* and *Nemacaulis*. *Nemacaulis* is similar to *E. gossypinum* in that both have copious bractlets and hairs surrounding and protecting the flowers; in *Eriogonum* the tubular involucre is broadly campanulate, but in *Nemacaulis* the involucre is lacking and replaced by subtending bracts. Beyond this, the two taxa are notably distinct. Still, it seems likely that the origin of *Nemacaulis* can be traced to *Eriogonum* subgenus *Ganysma* and, in particular, the section of *Ganysma* which contains *E. gossypinum*.

Looking upon *Nemacaulis* as a recent derivation from *Eriogonum*, it seems to have undergone rapid development in the hot

deserts of southern California and adjacent Mexico, occupying a position on the southern geographical edge of *Eriogonum* section *Ganysma*. I suspect the degree of difference between *Eriogonum* and *Nemacaulis* is on the magnitude of that exhibited by *Eriogonum* and *Oxytheca*.

The genus *Hollisteria* is a most difficult genus to trace back to its possible point of origin. It is a prostrate, spreading annual with two sessile, yellow, woolly flowers subtended by three slightly united involucre bracts. In some respects, *Hollisteria* is intermediate between *Eriogonum* and *Chorizanthe*. It differs from both in lacking a distinct involucre tube, but it is two-flowered and thus similar to *Centrostegia* and has acerose tips on the bracts similar to those on *Goodmania*. It probably did not evolve from an unknown perennial group as proposed by Stebbins (1974) but more likely developed from an annual complex.

I would like to say that *Hollisteria* could have evolved from either *Eriogonum* subgenus *Ganysma* or *Oregonium*, but no extant group in either subgenus can really point the way. I have tried to place the genus near *Chorizanthe*, but still no one group of that genus really is helpful. In some respects, I have tried to fit it into a pigeonhole between what Goodman termed *Eriogonella* (*C. membranacea* Benth.) and *Centrostegia* because here one can find a combination of three-lobed involucre, yellowish flowers, and a spreading annual habit. Still, one compelling bit of evidence that wrenches this entire scene is the nature of the pollen grain. As Nowicke (pers. comm.) has recently shown, the pollen grains of *Hollisteria* and *Lastarriaea* are essentially the same, and unlike any other genus of *Eriogonoideae*. It is possible that both *Hollisteria* and *Lastarriaea* evolved from an extinct, independent complex of annual species. One part of the complex close to *Eriogonum* could have given rise to *Hollisteria* while another part of the complex close to *Chorizanthe* gave rise to *Lastarriaea*.

As one might suspect from the foregoing discussion, the genus *Lastarriaea* is also somewhat intermediate between *Eriogonum* and the annual species of *Chorizanthe*, but closer to the latter than the former. *Lastarriaea* is a low, often spreading annual without a distinctly tubular involucre, acrose bracts, and whitish, glabrous, coriaceous tepals. Unlike all of the genera discussed to this point (with the exception of some species of *Chorizanthe* and *Nema-caulis*), *Lastarriaea* has only three anthers per flower instead of the usual nine. And unlike *Hollisteria*, which is an inland species of the Inner Coast Ranges of California, *Lastarriaea* is a coastal genus found in both North and South America.

Goodman (1934) placed *Lastarriaea* in *Chorizanthe* in the least specialized section of the genus, and, while there are some superficial similarities between the section *Suffrutices* Benth. and *Lastarriaea* to the point that perhaps it evolved from this section, I doubt that its point of origin can be traced to any extant section of *Chorizanthe*. As noted above, a more likely situation is that *Lastarriaea* developed early in the evolution of the annual species of *Chorizanthe* (or less likely, *Eriogonum*). I strongly suspect that *Lastarriaea* became well established in North America, and that it, the one annual species of *Chorizanthe*, and *Oxytheca* all migrated to South America at approximately the same time as hitchhikers on animals, probably during the Late Pliocene (Raven 1963). The differences between the North and South American elements are not strongly expressed morphologically in these annual species, although a strong difference does not necessarily have to be expressed (Grants 1967).

Mucronea is clearly derived from the annual species of *Chorizanthe*. This genus has a distinctly tubular involucre like *Chorizanthe*, but it and *Centrostegia* differ in having three-lobed bracts instead of the typically entire bracts of *Chorizanthe*. The conspicuous bracts of *Mucronea* are united and distinct, and in this feature the genus is sim-

ilar to *Eriogonum* and *Oxytheca*, especially *O. perfoliata*. *Mucronea* is distinct from *Centrostegia* and *Oxytheca* in having straight cotyledons (Goodman 1934), but is similar to *Chorizanthe* in this regard. I suspect that *Mucronea* is a rather recent innovation within the *Chorizanthe* complex.

The genus *Acanthogonum* was recognized as a distinct genus by Goodman (1955), but I am still somewhat reluctant to recognize it. When Torrey (1857) described *Acanthogonum*, he placed a single species, *A. rigidum*, in the genus. In 1858, Torrey questionably added a second species, *A. corrugatum*, noting that this species was "almost intermediate between *Acanthogonum* and *Chorizanthe*." Torrey and Gray (1870) reduced both species to *Chorizanthe* and added to the complex *C. polygonoides* and *C. watsonii*. Goodman (1934) defined *Acanthogonum* to include *A. rigidum* and *A. polygonoides* (Torr. & Gray) Goodman, and these two species were retained in the genus in his 1955 review. Basically Goodman maintained the genus on the basis of the curved cotyledons, but, as I am retaining *Eriogonella* in *Chorizanthe*, which was established (in part) on its curved cotyledons, I cannot very well recognize *Acanthogonum* because of this feature. For now, at least, the relationship between *C. polygonoides* and *C. corrugata*, *C. watsonii*, and *C. orcuttiana* Parry seems too close to allow for a distinct genus to be established.

Centrostegia is a most difficult and diverse assemblage of species. As defined by Goodman (1957), the genus consists of four species, three of which, *C. leptoceras* A. Gray, *C. thurberi* Gray ex Benth. in DC., and *C. vortriedei* (Brandeg.) Goodman, form one distinct element within the genus, but *C. insignis* is decidedly aberrant although even *C. vortriedei* is somewhat strange within *Centrostegia*. I am inclined to restrict *Centrostegia* to *C. thurberi* and *C. leptoceras* but am lost when it comes to *C. vortriedei*, and feel *C. insignis* should probably go into a distinct genus. This latter species is certainly most closely related to *Oxytheca*,

where Goodman (1934) placed it at one time. As for *C. thurberi* and *C. leptoceras*, one might look for an origin somewhat intermediate between *Eriogonum* and *Chorizanthe*. Until these species can be carefully studied, especially cytologically, little can be expressed about their relationships. I have little faith in the one unifying character, which is the three-lobed bract, and would like to place more emphasis on the involucre, floral, and vegetative features of these plants.

Up to this point, the discussion has centered on the tribe Eriogoneae, which makes up the vast bulk of Eriogonoideae. The other tribe of the subfamily, Pterostegae, contains only two monotypic genera. Time and evolution have largely destroyed the interconnecting links between the two tribes so that it is impossible to say what, if any, role Eriogoneae might have played in the evolution of Pterostegae, or the other way around for that matter. The inflated bracts of the fruiting specimens are unseen in Eriogoneae, and the consistently opposite leaves are rare. I suspect that the two tribes are well separated now by time and events.

Until Parry's (1886) paper in which the genus *Harfordia* was described, the true nature of this narrowly restricted shrub was unknown. Benthams (1844) had placed the perennial in the genus *Pterostegia* not knowing if his species, *P. macroptera*, was a shrub or not. It remained there until 1886. Only Roberty and Vautier (1964) reduced *Harfordia* to *Pterostegia*. In spite of this, there is little reason to closely associate *Harfordia* with *Pterostegia* except in the feature of the fruiting bracts and opposite leaves.

Hutchinson (1926, 1959, 1969) was a firm believer in the concept that certain families of flowering plants were fundamentally herbaceous or woody. Polygonaceae, in his view, was basically a herbaceous group in which the woody, or shrubby, condition was a secondary state. There is something to say about this point, although it may seem contrary to the usual dicta (Bessey 1915). The largest forms of *Eriogonum*, for example,

are highly derived forms from low, sub-shrubby or shrubby groups. *Eriogonum austrinum* (S. Stokes) Reveal is an annual species that will form perennial individuals, and this is a condition that will be seen in other species as well. The reason to bring this controversial subject up is *Harfordia*, the perennial, versus *Pterostegia*, the annual. It is possible that *Harfordia* represents the residue of an ancient series of events in a perennial line of evolution from which, at some time in the past, the ancestral fore-runners of *Pterostegia* evolved. This is the reasonable approach. Another which cannot be totally ignored is that *Harfordia* is a secondarily evolved perennial which developed from an annual group in order to survive in the extreme stress of long-term drought associated with the environment of central Baja California. *Pterostegia* is basically a mesic species, and I do not propose to imply that *Harfordia* evolved from *Pterostegia*, but anatomical and cytological studies may be helpful in unraveling this question.

SUMMARY

The subfamily Eriogonoideae is divided into two tribes, Eriogoneae and Pterostegae, which are somewhat atypical members of the Polygonaceae. The subfamily is restricted to the more xeric areas of central North America and western South America. The basic extant expression in the subfamily is *Eriogonum*, whose ancestral roots can probably be traced to the tropical or subtropical members of the family. *Chorizanthe* was a major side-shoot from *Eriogonum*, and from these two fundamental genera have evolved a series of small, usually closely related genera. *Eriogonum* and the perennial forms of *Chorizanthe* probably developed in the pygmy woodlands of the Madro-Tertiary geoflora, with the related genera evolving mainly in the more xeric, hot deserts at elevations lower than those in which *Eriogonum* is typically found.

The largest and most diverse genus is *Eriogonum*, both in terms of numbers of

species and in expressions. *Chorizanthe* is the next largest, but the degree of morphological divergency in this genus is not as great as in *Eriogonum*. As for the remaining, smaller genera, each attempts to fill an available morphological gap or ecological niche, and for the most part, each is successful.

Much work remains to be done on the subfamily. The South American species of *Chorizanthe* must be studied in the field. The nature of the relationship between the South American perennials and the North American annuals of this genus must be determined, and then, if the two should prove distinct, we must decide by what name the annuals should be called. Field studies are now critically needed so that anatomical and cytological material can be gathered, and perhaps greenhouse investigations made. A series of monographic studies are now in progress, mainly on the genus *Eriogonum* and its immediate relatives. In time, these studies must be expanded beyond the alpha taxonomic level where they are now. This will be a continuing challenge to anyone wishing to travel, study, and investigate one of the world's most unique groups of flowering plants.

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league, Dr. C. Rose Broome, of the University of Maryland, for sharing with me her ideas and thoughts on the complex problems of evolution and speciation as they might apply to *Eriogonoideae*.

NOTE ADDED IN PROOF

Since this manuscript was completed in June 1976, the revision on *Oxytheca* has been completed [ERTTER, B. J. 1977. A revision of the genus *Oxytheca* (Polygonaceae). Unpublished Master's Thesis, University of Maryland Library, College Park] and a number of minor changes must be appended. Ertter found that *Oxytheca* consists of seven (not nine) species, with the "South American form" being merely a subspecies of *O. dendroidea*, and the "new species" from the San Bernardino Mountains of California a variant of *O. parishii*. Ertter concurs that *O. dendroidea* and *O. watsonii* are related to *Eriogonum spergulinum*, and she has shown conclusively that *O. perfoliata* is clearly related to *O. dendroidea*. In fact, *O. watsonii*, a rare species of west-central Nevada, is intermediate between *O. dendroidea* and *O. perfoliata* in many respects according to Ertter.

Ertter also concurs that *Oxytheca parishii* is most closely related to *Eriogonum apiculatum* and *E. parishii*, but in doing so called attention to an error in my own work on *Eriogonum* (Reveal 1969a). In my revision of *Eriogonum* I placed *E. spergulinum* and *E. apiculatum* in widely separated sections of the subgenus *Ganysma*. Ertter has shown that these two species complexes are much more closely related than I had thought. In the present paper I raised the question that if *O. dendroidea* and its allies arose from the *E. spergulinum* complex (in one part of *Ganysma*), and *O. parishii* arose from *E. apiculatum* (in another part of *Ganysma*), then perhaps the genus *Acanthoscyphus* should be recognized. Such a situation now is unnecessary.

The relationship between *Oxytheca parishii* and the remaining members of the

genus in southern California (*O. caryophylloides*, *O. trilobata*, and *O. emarginata*) is still tenuous. Ertter has shown, however, that *O. parishii* is more similar to the *O. dendroidea* complex than it is to the *O. caryophylloides*. She has proposed to place *O. dendroidea*, *O. watsonii*, and *O. perfoliata* in their own typical section, with *O. parishii* in a monotypic section. As for the other three species, these are going into a third section, a taxon somewhat removed from the other sections.

I still believe that the southern California elements evolved as a group in the mountainous regions of southern California during the Pleistocene, but I now feel that this development came not from isolated elements with *Eriogonum* but from a broadly connected group of annual species all belonging to this one genus which were undergoing collectively rapid evolution (see Raven and Axelrod discussed below).

As for the troublesome *Centrostegia insignis*, recent conversations with Goodman confirm the supposition that this species is seriously out of place in *Chorizanthe* (Goodman 1934), *Oxytheca* (Ertter 1977, cited above), and even *Centrostegia* (Goodman, pers. comm.) and that it most likely will have to be placed in its own monotypic genus. This question is now being explored.

Nowicke's pollen work discussed above has now been published [Nowicke, J. W., AND J. J. SKVARLA. 1977. Pollen morphology and the relationship of the Plumbaginaceae, Polygonaceae, and Primulaceae to the order Centrospermae. Smithsonian Contr. Bot. 37: 1-64.].

Lastly, my manuscript has been used by Drs. Peter H. Raven and Daniel I. Axelrod in a book entitled *Origin and Relationships of the California Flora* published by the University of California Press. Based upon my review of their manuscript (which should be published at approximately the same time as this volume), their work will nicely complement the present volume.

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PROBLEMS IN PLANT ENDEMISM ON THE COLORADO PLATEAU

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ABSTRACT.—The problem of distribution of plant endemics is explored, especially as regards distribution of these plant species on elevational and substrate bases. Endemics per unit area are greater at elevations above 1980 m and on finely textured soils. A summary of data and a list of references is presented.

The Colorado Plateau has long been known as a center for endemic plants. The basis for that endemism most certainly involves the unique features of the Plateau Province, especially as regards climate, geological history, and position along migratory routes. Each of these features has played a role, and the interpretation of the nature of endemism in the region must reflect the part each has played. Climate is considered as arid for the region generally, but the mountains within and bordering the Province stand as moist discontinuities in this arid middle portion of the Colorado River drainage system. Geology is, in large part, displayed in technicolor, with Mesozoic and Cenozoic strata dominating, and with the thin cover of vegetation hardly obscuring the geology. Only at higher elevations is the mantle of vegetation sufficiently dense as to cloak the geological substrate. Volcanic intrusives and extrusives are limited in area. Sedimentary formations constitute the main features of the plateau region.

Canyons of grand size are entrenched into the surfaces of the uplifted plateau, where formations are displayed along the margins of horizontal or gently dipping plateaus. Broad anticlines, synclines, or gentle to steeply plunging monoclines have been eroded to expose hogbacks or cuestas where vast stratigraphies are exposed in relatively short distances.

Main migratory routes into the plateau involve the mountain sequences in the Rocky Mountains along both the eastern and western margins. The great river system has provided a lane for movement of propagules both up and down stream. Great Plains influence appears to have been mainly from the southwest. Hence, the flora of the plateau is a function of the sources of its plants; Mohavean, Chihuahuan, Great Plains, Rocky Mountain, Great Basin, etc.

My own interest in plant endemics within the Colorado Plateau began more than two decades ago when I began research leading to a thesis on the vegetation of the Utah portion of Dinosaur National Monument (Welsh 1957). The geological control of vegetation at lower elevations in the plateau is readily apparent, but nowhere so overwhelming as along the margins of the Split Mountain anticline at Dinosaur National Monument. The interaction of various substrates to low annual precipitation through long periods of time has led to the demonstration of edaphic differences on a grand scale. Soil formation in a traditional sense is unknown. The substrate surface is often merely residual parent material only slightly modified from that a few inches below the surface. Alluvium and colluvium function differently from residual or parent materials.

Conditions for growth on the substrates

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available are often rigorous at best. Frequently, those plants capable of establishment and reproduction are few in number. Competition is therefore limited, with the harsh environments supporting very few higher plant species.

This point is illustrated by a statement ascribed to the venerable Walter P. Cottam concerning vegetation of the Mancos Shale formation. While camped on that formation, he is reported to have stated that, "there were only four species of plants growing here, and I don't know three-fourths of them." This statement, whether true or not, is indicative of the paucity of vegetation on some of the formation, and of the peculiar nature of some of the entities growing there.

Worst possible substrates available are the clays derived from saline shales such as members of the Mancos Formation and its counterparts such as the Tropic Shale (Tununk equivalent). Salt contents of 30,000 ppm are not uncommon. Additionally, the clays perform in a special manner when water is added. A rainstorm of some six hours' duration supplied from 2 to 6 inches of water in June 1972 to the Tropic Shale east of Glen Canyon City in Kane County, Utah. Penetration into the clay of the Tropic Shale did not exceed 2 inches. Even when wet to field capacity the clays provide very little moisture for plant growth. Still, a few plants do grow on this substrate, some of them continuing to flower and to mature fruit at soil moisture levels below the arbitrary 15 atmosphere level accepted as the permanent wilting point.

At higher elevations, where rainfall is greater, even these substrate types are overwhelmed by vegetation and a soil mantle is developed which eventually is effective in insulating the vegetative cover from the effects of high salinity and from such substances as selenium.

Sandstones and their derivatives form the other extreme in edaphic situations. Soluble salts are fewer, selenium is more restricted, water penetration is greater, and the pro-

portion of water which can be extracted from soil at field capacity is greater. Increased species diversity on sands is apparently a function of the greater ease of establishment and better all-around water and soil relationships, given equal elevation, temperature, humidity, and opportunity for establishment.

Glaciation has apparently not played a major role in the plateau, except in the highlands along its fringes. Persistence of plants through the Pleistocene has been a possibility in at least the lower elevation portions, and indeed in most of the Plateau Province.

With this background, it seems both feasible and necessary to attempt to quantify the data on endemism. The data have been generated from information recorded on herbarium labels of specimens deposited at Brigham Young University and at the National Museum of Natural History, Smithsonian Institution. Further data have been taken from various taxonomic treatments (see list of references). Despite all attempts, the information available is fragmentary, and the conclusions derived from that information must be regarded as tentative. A portion of the problem involves the nature of endemics generally. Some of them are highly restricted and they have been collected only once or a very few times. Information on substrate, elevation, geological formation, and other pertinent information is not available either on the herbarium materials or in the literature. Further, most plant taxonomists (and others who collect plants) are not well prepared in identification of substrate types. The clays and silts of some investigators will be the sands and gravels of others. Despite the shortcomings of the information, there seem to be trends which can form the basis for further investigations.

The data summarized from the sources investigated are presented in Table I. Only 34 families of vascular plants are known to have endemic species in the region. The total number of endemic entities is some 340,

an average of about 10 per family. The endemics are far from equally divided among the various families. The Boraginaceae (20), Compositae (58), Leguminosae (86), Polygonaceae (28), and Scrophulariaceae (29) contain some 221 species or about 65 percent of all endemic taxa. The greatest number of taxa occurs in the Legume family. The 86

entities constitute some 25 percent of all of those in the region.

The genus *Astragalus*, with 62 endemic taxa, is not only the largest single contributor to the list of endemics, but contributes a greater number of taxa than any family beside the legumes. Most of those taxa occur at low elevations, contributing to the

TABLE 1. Summary of plant endemics on the Colorado Plateau

Family Name	Taxa No.	Substrate				1980 m <6500 ft	Elevation 1980m		Both	NA
		C, S, M	Sand, G	Both	NA		>6500 ft			
Apocynaceae	4	1	3	1		4				
Asclepiadaceae	4		2	2		2	1			
Boraginaceae	20	3	7	10		9	3		4	4
Cactaceae	11	2	1	2	6	5				6
Capparidaceae	1			1		1				
Caryophyllaceae	1	1					1			
Chenopodiaceae	6	2	2	1	1	4			2	
Compositae	58	9	29	4	16	25	12		7	14
Cruciferae	11	6	3	2		7	4			
Cyperaceae	5		3		2	2	3			
Elaeagnaceae	1		1						1	
Ephedraceae	1		1			1				
Euphorbiaceae	1	1				1				
Gramineae	2		2				2			
Gentianaceae	2			1	1	1			1	
Geraniaceae	1		1				1			
Hydrophyllaceae	12	6	3	1	2	9			1	2
Labiatae	2			2		1	1			
Leguminosae										
Astragalus	62	18	35	9		42	16		4	
others	24	5	17	1		16	4		3	1
Liliaceae	4		4			3	1			
Najadaceae	1		1				1			
Nyctaginaceae	2		2			2				
Onagraceae	9	3	6			6	2		1	
Papaveraceae	1		1			1				
Polemoniaceae	13	3	10			5	5		2	1
Polygonaceae										
Eriogonum	27	14	12	1		17	8		2	
Other	1		1				1			
Portulacaceae	1		1			1				
Primulaceae	1		1			1				
Ranunculaceae	6		6				4		2	
Rosaceae	1		1			1				
Rubiaceae	2		2			1			1	
Scrophulariaceae	29	7	21	1		8	13		8	
Selaginellaceae	1		1			1				
Umbelliferae	12	3	9			5	5		2	
Total	340	84	187	40	29	182	88		41	29
Percentage		24.7	55.0	11.8	8.5	53.5	25.9		12.1	8.5

Abbreviations: C, clay; S, shale, M, mud; G, gravel; NA, not available.

idea that endemism is especially great at low elevations. Despite this apparent abundance of endemics at low elevations, only slightly more than half of the entities are known from below 1980 m (6500 feet) in elevation; a quarter of them occur above 1980 m (6500 feet), 12 percent overlap, and 8.5 percent are unknown. However, the total land area above 1980 m in elevation represents only about 30 percent of the region. When endemics are expressed in per unit area figures there is 1 endemic per 1170 km² for the higher elevations and 1 per 1318 km² below that elevation. Thus, the incidence of endemics generally is greater at the higher elevations.

The area of the Colorado Plateau is roughly 340,000 km² (133,000 sq mi), which places the density of endemics at about 1 per each 1000 km². Almost half (55%) of the endemics occur on sand and gravel, and a quarter on clays, shales, or muds. Those that grow on both types constitute only 11.8 percent, and data is missing for some 8.5 percent.

It is difficult to derive data on the proportions of sands and gravels to other substrate types. Certainly the sands and gravels cover more of the land surface than do the other substrate types. If one assumes that only a quarter of the included region consists of clays, shales, and muds, then the endemics on clays occur at about 1 per 1000 km². Those on sands and gravels are present at a density of only 1 per each 1350 km².

Initial impressions by collectors that endemics are especially rich on the finely textured soils are supported by the fabricated data. Certainly if the total area occupied by clays is less than 25 percent, then the endemics per unit area might be expected to be very great indeed. Surprising is the greater density of endemics in the montane sections of the plateau. Distribution of endemics is hardly at random, and any attempt to provide averages or taxa per unit area is likely to obscure the geographic controls which result in the development and placement of the taxa.

In a previous paper (Welsh, Atwood, and Reveal 1975), the endangered, threatened, extinct, endemic, and rare or restricted vascular plants of Utah are plotted by geographic subdivision of the state. The large part of those plants represent endemic plants of Utah. Instructive from the plotting is the apparent unequal distribution of those plants in the state. Main centers of distribution include the high plateaus of south central Utah, the Canyonlands section, and the Uinta Basin. A trend is present, however, which indicates that the greater numbers occur near the southern end of Utah, with progressively fewer taxa northward.

Since endemic plants are likely to be considered as endangered or threatened, and since most of the lands within the Colorado Plateau are federally controlled, then some management of these specialties is indicated. Perhaps it is possible to establish some predictive guidelines with regard to location of endemics (i.e., where they might be expected to occur). Outcrops of shale, mudstone, and siltstone at all elevations should be considered as suspect sources for plant endemics. Any peculiar substrate, such as the lacustrine limestones at higher elevations in the western margin of the plateau, should be considered as important localities for endemic taxa. Glaciated localities can generally be excluded from consideration in management practices.

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SOME FACTORS GOVERNING PLANT DISTRIBUTIONS IN THE MOJAVE-INTERMOUNTAIN TRANSITION ZONE

Susan E. Meyer¹

ABSTRACT.—The existence of a floristic transition zone can be inferred by the fact that a high proportion of indigenous plant species reach a distributional limit within the area. The vascular flora of Washington County, Utah, exhibits this character to a marked degree with 53.6 percent of the native flora reaching a distributional limit within the county. By looking at geographic distributions, ecological preferences, and range termination information for the component species, first approximations are made as to the probable factors mediating plant distributions within the county, particularly of the range-terminating species. The high proportion of range-terminating species in the flora may be accounted for mainly by limiting factors associated with abrupt shifts along two environmental gradients. The first factor is climatic and is mediated largely by altitude; change occurs primarily along a north-south gradient. The second is both climatic and edaphic and is mediated by factors other than altitude per se; it is oriented in an essentially east-west direction. Species with narrower tolerances are shown to be more sensitive to these environmental shifts. Some of the species distributions are better explained by a model involving the effects of interactions between habitat mosaic and genetic homogeneity of given populations on relative migration rates in the transition area. These species may have the capacity to migrate farther, but differences in migration rates give their distributional limits a quasi-stable aspect. These data suggest that species cannot simply be divided into those which are environmentally limited in their present distributions and those which are not. It seems more fruitful to regard these two conditions as extremes on a continuum which can be expressed as migration rate.

A floristic transition zone is characterized by the range termination of a high proportion of the indigenous species. The vascular flora of Washington County, Utah, exhibits this character to a marked degree, with 53.6 percent of the 1,067 indigenous species reaching a distributional limit within the county. The objectives of this study are to obtain detailed documentation of plant distributions within the transition area, to identify environmental factors that might be controlling range limits, and to elucidate relationships between the distribution patterns of groups of species and their ecological amplitude.

Early observations on the floristic transition zone as it occurs in Washington County include those of Parry (1875), Merriam (1893), and Jones (1910). The nature of the

zone as it occurs in Nye County, Nevada, has been examined in some detail by Beatley (1975), while Bradley (1967) has published a phytogeographic survey of Clark County, Nevada, which also lies along the zone. Additional Washington County observations include those of Hardy (1947), Cottam et al. (1959), and Woodbury (1933). Whittaker and Niering (1964) worked with problems of a similar nature in southern Arizona.

DESCRIPTION OF THE STUDY AREA

Washington County is located in the extreme southwestern corner of Utah. It is a roughly rectangular area which spans an east-west distance of about sixty miles and a north-south distance of about forty miles. A

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region of great environmental diversity, the county contains extensive outcrops of carbonate rocks, sandstones, shales, and both extrusive and intrusive igneous rocks (Cook 1960). Elevations range from about 2,000 feet (600 m) near the common boundary with Arizona and Nevada to over 10,000 feet (3100 m) at the top of the Pine Valley Mountains to the north. The dramatic nature of the landscape is exemplified by Zion National Park, most of which lies within the county.

These diverse environments are not mingled randomly; they represent instead the junction and interdigitation of three larger land areas which are themselves relatively homogeneous. Figure 1 shows the geographic position of the county relative to these areas and to the boundaries which separate them.

The first of these boundaries separates the Basin and Range Province from the Colorado Plateau Province. These two areas are very different both lithologically and in the relative proportion of high to low land. The former is comprised of isolated mountain ranges composed mainly of carbonate rocks separated by broad, alluvium-filled valleys. The latter is comprised of a contiguous series of high plateaus composed mainly of sandstone and shale, with lower elevations restricted mainly to relatively narrow canyon floors. The climate of the Colorado Plateau, as a whole, is more mesic than that of the Basin and Range Province. The transition between these two physiographic provinces takes place within the county.

Superimposed on this boundary is another boundary, which is designated on Figure 1 as the 4,000-foot contour line. Valley floors to the north of this line consistently lie above 4,000 feet and thus have a climate which is comparatively cold. Valley floors to the south always lie well below 4,000 feet and thus have a climate which is warmer. The line effectively divides the Basin and Range Province into two subregions, the Great Basin region to the north and the desert lowland region to the south. The fact

that part of Washington County lies south of this line indicates an attenuation of desert lowlands along the Virgin River drainage into an area of generally higher land.

METHODS

The data presented here are summarized from an annotated checklist of the vascular plants of the study area (Meyer 1976). The systems of vegetational and floristic classification used here are more fully explained there.

Each species was assigned to one of thirty-eight floristic groups on the basis of published distributional information. A floristic group is considered as an assemblage of species which share a similar geographic distribution, without historical or ecological implication *per se*.

The floristic groups are here classified into two types of distribution patterns. An areal distribution classification aggregates the floristic groups into five classes on the basis of their areal extent. The directional distribution classification combines the flo-

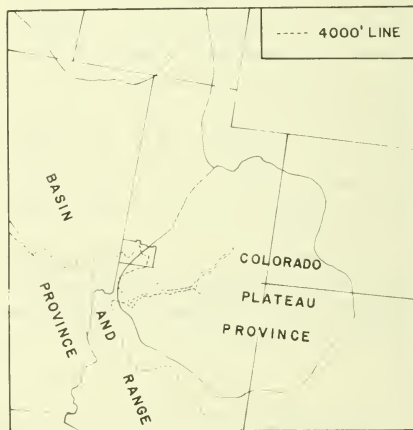


Fig. 1. Location of Washington County, Utah, relative to state and physiographic boundaries and to the 4000-foot contour line.

ristic groups into seven classes on the basis of their main area of distribution relative to the study area. Introduced plants are not included in the tabulations.

All species which are reported to reach a distributional limit within the county are designated as range-terminating species.

The occurrence of each species in the nine major community types within the county was determined from field notes, herbarium specimens, and monographic sources.

It is assumed here that the occurrence of a species in a particular community type indicates something about its ecological amplitude and more specifically about the climatic tolerance of the species. That is, the characteristic and the dominant plants of each community type are considered to be indicators of climate. It seems better to use community type as a climate indicator rather than elevation, because of the effect of local modifying factors on the relationship between elevation and climate. It would be even better to monitor environmental factors directly, but this was logistically impossible.

In order to measure the degree of habitat specialization exhibited by various segments of the flora, a fidelity index is used:

$$FI = \frac{\frac{\text{total species in segment}}{\text{total community occurrences in segment}}}{\frac{\text{total species}}{\text{total community occurrences}}}$$

The values in this equation are derived in the following way. Each species in the flora occurs in one to nine possible community types. The value of the denominator equals the total species number (1067) divided by the total number of community occurrences (2182), or 0.489, indicating that the average species in the flora occurs in approximately two community types ($0.489 \approx \frac{1}{2}$).

The value for the numerator is derived in similar fashion, using total species number divided by total community occurrence

number for any subcategory or segment of the total flora. For example, the value of the numerator for the endemic class is 0.606 (83 species in segment divided by 137 total community occurrences).

The value of FI is defined as unity for the total flora, since in that case numerator and denominator have the same value. The value of FI for the endemic class would be 1.24 (0.606 divided by 0.489). Since this value is greater than unity, the endemic class shows a higher degree of habitat specialization than the flora as a whole. Values smaller than unity values would indicate the converse.

Given a value of 0.489 for the denominator, the value of FI can range from 0.23 (0.111 or one-ninth divided by 0.489) to 2.05 (unity divided by 0.489). These two extremes represent the respective cases of the average species in the segment occurring in all nine community types (one species/nine community occurrences) and in only one (one species/one community type).

Species which appear to be limited to a single substrate are designated as edaphically restricted species. Halophytes are not included in the edaphically restricted category because halomorphic soils develop on a variety of substrates.

FACTORS GOVERNING MIGRATION RATES

Propagule dispersal is a stochastic process. A plant disperses propagules in all directions, regardless of whether the propagule is likely to be dispersed to a site favorable for its growth, or whether an effective dispersal constitutes a range extension for the species.

An effective dispersal is accomplished when a propagule is dispersed to a site for which it is preadapted in terms of genetic tolerance (Good 1930) and is therefore able to grow and reproduce. When this site falls outside the previous distributional area for the species, the process is called migration.

Effective dispersal (and thus migration) is a function of three sets of variables. These

are distance, size of population supplying propagules, and time. Their operation is based simply on the laws of chance. The first two variables may be related to the third as an expression of rate. The rate at which a species is able to migrate is a function of effective source-population size and of average minimum dispersal distance (the average minimum distance a propagule must be dispersed in order to arrive at a site for which it is preadapted). The larger the effective source-population size and the shorter the average minimum dispersal distance, the higher the migration rate.

Populations adjacent to the area of potential colonization are more likely to disperse propagules into the area than those located at greater distances. Therefore, the rate of migration into an area is most influenced by properties of populations immediately adjacent to that area.

The size of effective source-population is conditioned by several factors: 1) absolute size and density of the population, 2) reproductive efficiency, and 3) dispersal efficiency. These simply say that the chance of propagules being dispersed to sites for which they are preadapted is increased if more propagules are produced and if propagules can disperse more efficiently.

Minimum dispersal distance is the same for all propagules produced by a population only when they are all preadapted to identical sites. More often, minimum dispersal distance is different for different propagules because of their preadaptation to different environments. The average minimum dispersal distance represents a mean value for all the propagules produced. It is dependent upon three sets of factors: 1) environmental heterogeneity, 2) amount of genetic heterogeneity for tolerance characters present in the population, and 3) degree of congruence between environment and tolerance characters of the dispersed propagules.

If the environment is homogeneous and favorable, the average minimum dispersal distance will be very short, and migration will be relatively rapid. If the environment

is homogeneous and unfavorable, the average minimum dispersal distance will be very long and migration will be relatively slow. Furthermore, these effects will increase with the degree of genetic homogeneity of the population.

Thus a population with narrow tolerance (low genetic heterogeneity) will be able to migrate rapidly through an environment which is homogeneous and favorable because of the very high probability that a propagule will be dispersed to a site for which it is preadapted. But its rate of migration through an environment which is homogeneous and unfavorable will approach zero, because of the very low probability that a propagule will be dispersed to a site for which it is preadapted.

A population with broad tolerances (high genetic heterogeneity) would be able to migrate less rapidly than a species with narrow tolerances through an environment which is homogeneous and favorable. This is because of the production of some propagules preadapted to conditions other than those present in the homogeneous environment. It would, however, be able to migrate more rapidly through a homogeneous and unfavorable environment. This is because it produces propagules preadapted to a wider variety of environments, and thus some propagules are likely to be preadapted for survival in the potential migration area.

A heterogeneous environment is made up of a mosaic of different environments. A genetically heterogeneous population will produce propagules preadapted to a wide range of environments, and thus a high proportion of the heterogeneous environment will be "read" as favorable by the average propagule it produces. This means that the average minimum dispersal distance will be relatively small and thus that migration will be relatively rapid.

A genetically homogeneous population will produce propagules preadapted to a narrow range of environments; hence a low proportion of the heterogeneous environment will be read as favorable. Average

minimum dispersal distance will be relatively large, and migration will be relatively slow.

This model is attractive in its simplicity but is lacking in several respects. Most importantly, it does not take into account the fact that both the genetic constitution of the population and the environment may themselves be changing through time. In effect, it is an instantaneous rate expression; it simply describes the options at a given point in time. In nature the situation is complicated by the fact that several of the variables in the rate expression may themselves be changing.

A change in the environment might change the configuration of favorable and unfavorable sites for a population and thus alter its migration rate. In some cases sites already occupied might become unfavorable, causing a diminution in range. Such secular climatic changes are well documented in the general area under discussion (Mehring 1965, Mehring and Martin 1965). It is important to consider that a species may have attained its modern distribution under environmental conditions very different from those now prevailing.

The genetic constitution of a population is subject to change from several sources. Two of these, gene flow and selection, are particularly important in this discussion. The former would tend to have the general effect of increasing heterogeneity. The latter could have one of three effects. In a homogeneous and constant environment, normalizing selection would tend to decrease variability. In a homogeneous but progressively changing environment, directional selection would tend to produce an adaptive shift, providing that the original population was sufficiently variable. In a spatially heterogeneous environment, disruptive selection could operate to produce genetically differentiated subpopulations, particularly if gene flow between subpopulations were minimized. These sources of genetic change are especially important in an area such as the one studied, which

meets the criteria of Stebbins (1974) for an area in which active speciation may be expected to be proceeding. It is also an area in which much of the habitat is hybrid-inducing in the sense of Anderson (1949). Many otherwise allopatric species have distributions which overlap in this area; they can often be observed to introgress or intergrade, depending on the viewpoint as to their origins.

In spite of the shortcomings of the model of migration rate presented above, it is quite useful in interpreting Washington County data.

DISCUSSION OF DATA

For interpretive purposes, two sorts of information about each species are examined. One involves the distribution pattern for the species as a whole. The other involves ecological factors which govern its distribution within the transition area. When these two sets of information are examined together, a high correlation between geographic distribution and particular ecological requirements becomes apparent.

Table 1 shows the percent contribution of each of seven distributional classes to the range-terminating group as compared to the total flora. It can be seen that the classes do not contribute equally to these two groups. The Mojave, Colorado Plateau, and endemic classes contribute far more than their share to the range-terminating group, making up almost 70 percent of this group but comprising only about 40 percent of the total flora. These differences are made up partially by the northern class, which is notably underrepresented in the range-terminating group.

Column three of Table 1 shows the percentage of species contained within each distributional class which are range-terminating. This value is almost 100 percent for the endemic and Mojave classes, indicating that a high proportion of the species may have reached a point which necessitates migration through an environment that is

homogeneous and unfavorable. This possibility is reinforced by the fact that they show high fidelity indices, indicating a high degree of habitat specialization and thus a low degree of genetic heterogeneity for climatic tolerance characters.

The Colorado Plateau and Great Basin classes also show a relatively high percent of range-terminating species, indicating a higher sensitivity to the environmental transition between the Colorado Plateau and the Great Basin than might have been expected. In fact, these two classes account for almost a third of all range-terminating species, a contribution almost as great as that of the Mojave class.

The southern class also shows a high proportion of range-terminating species, but the converse is true of the northern group. These apparently do not read the environment to the south of the county line as homogeneously unfavorable. One explanation for this is the fact that the northern class is not as specialized ($FI = < 1$) and thus should be able to migrate more effectively through a heterogeneous or even homogeneously unfavorable environment. Another possibility is that these species attained their distributions at some time in the past when environment was more homogeneously favorable.

The range-terminating members of the northern class have a much higher fidelity index than the class as a whole. These species would presumably have trouble mi-

grating through the heterogeneous environment of the transition zone because, due to their genetic homogeneity, they tend to read more of it as unfavorable. In fact, the range-terminating members of a class consistently show a higher fidelity index than the class as a whole, lending credence to the concept that low genetic variability for tolerance characters makes migration across a transition zone more difficult.

Table 2 shows the percentage contribution to each community type and to the total flora by each of the seven directional distribution classes. The community types are arranged roughly in altitudinal sequence.

The nondirectional class is slightly to markedly overrepresented in every community type except the Hot Desert Shrub community. In general, the species have broad tolerances and occur in a variety of community types, a fact also evidenced by their low fidelity index (0.79).

About 85 percent of the Mojave species occur in the Hot Desert Shrub community, making up almost half of the total flora. Perhaps more significant is the fact that an appreciable percent of the species in two of the higher elevation communities, Foothill Woodland (11 percent) and Mountain Brush (6 percent) is comprised of Mojave species. Bearing in mind that over 98 percent of the Mojave species are range-terminating, it is clear that some of these species (almost 20 percent of the total Mojave class) reach a

TABLE 1. Range termination and fidelity indices by directional class.

Directional Class	% Total Native Flora	% of Total Range-Terminating Species	% Range-Terminating Species in Class	Fidelity Index Total Class	Fidelity Index Range-Terminating Species
Endemic	7.8	14.0	96.4	1.24	1.24
Nondirectional	25.5	<1.0	<1.0	0.79	—
Mojave	17.6	32.3	98.4	1.32	1.34
Colorado Plateau	14.3	22.2	83.0	0.86	1.12
Great Basin	6.6	8.4	68.6	1.26	1.46
Northern	20.5	13.5	35.2	0.96	1.22
Southern	5.5	8.6	83.1	1.04	1.09
Anomalous	2.2	1.0	—	—	—
Total Flora	100.0	100.0	53.6	1.00	1.23

termination of range in spite of the fact that their tolerance characters permit some individuals to disperse successfully to higher elevation community types.

Most of the Mojave species have their main area of distribution in terms of numbers of individuals in the Hot Desert Shrub community. Their occasional anomalous occurrence in higher elevation community types indicates a broader climatic tolerance than that of species sharply restricted to the hot desert. Such species should be able to migrate through the ecotonal area because they can read at least some of it as favorable. Therefore, there seems to be no *a priori* reason for them to reach a limit of range in Washington County. Several factors might operate, however, to make their rate of further migration very slow.

Even though hot desert populations might be large, propagules preadapted for high elevation community types might be produced at very low frequencies. In addition, populations occurring in higher elevation communities might have lowered reproductive efficiency, thus retarding the establishment of large populations which could produce a higher frequency of preadapted propagules. Both factors would have the effect of keeping the effective source-population small.

The migrating species might be able to occupy only a portion of the sites within the higher-elevation vegetation types; the proportion of favorable sites might decrease with increasing distance from the transition zone. This could be true if the species were

only marginally tolerant climatically, if it had a narrow tolerance for some other environmental factor, or if it faced a competitive disadvantage in the presence of some high elevation species. All of these factors would have the effect of increasing the average minimum dispersal distance by increasing the proportion of unfavorable sites. Finally, the species may actually have migrated beyond the transition zone, but in such small numbers as to have escaped detection. In any case, the complex dynamics of the situation make it impossible to divide range-terminating species neatly into those which are limited by environmental factors and those which are not.

The community contributions of the remaining classes are easier to interpret. Since Rocky Mountain species enter the county via the Colorado Plateau, it is not surprising that the Colorado Plateau class is well represented in montane communities, particularly those of middle elevations. Many of these montane species reach a western limit of range, probably because of the much lower proportion of favorable sites and the much larger average minimum dispersal distances involved in migrating across the Great Basin. The class as a whole is underrepresented in Hot Desert communities, and most species which do occur there are not range-terminating. The important role played by edaphic factors in this class will be discussed later.

Very few of the Great Basin species enter the county at all; many reach southern and eastern range limits a few miles northwest

TABLE 2. Percent composition of plant communities by directional class.

Directional Class	% Total Native Flora	% Hot Desert	% Cold Desert	% Desert Riparian	% Foothill Woodland	% Mountain Brush	% Transition Forest	% Mountain Forest	% Mountain Riparian	% Mountain Meadow
Endemic	7.8	6.6	7.0	2.9	10.1	8.2	7.8	4.7	2.7	4.6
Nondirectional	25.5	16.2	34.9	39.4	31.2	33.7	37.0	33.2	40.5	31.8
Mojave	17.6	46.0	9.5	17.3	10.7	5.8	1.0	1.0	1.4	0
Colorado Plateau	14.3	9.2	14.0	9.0	15.8	17.3	21.9	15.8	12.2	12.1
Great Basin	6.6	6.6	7.0	5.1	6.4	5.8	2.7	5.3	3.2	1.0
Northern	20.5	4.0	18.1	14.4	15.4	23.1	25.1	37.9	36.9	50.5
Southern	5.5	9.0	7.0	9.4	6.7	3.4	2.7	1.0	1.4	0
Anomalous	2.2	2.3	2.5	2.5	3.7	2.9	1.8	2.1	1.8	0

of the county line. Those which do enter the county show a high degree of habitat specialization, but, oddly enough, this specialization is not to any particular community type. Classic Great Basin salt desert does not occur in Washington County, which may account for the disproportionately high representation of Great Basin species in other community types. Also, the total number of species is so small that a difference of a few species has a relatively large effect on the percent values.

As would be expected, species of the northern class are abundantly well represented in high montane communities, reasonably well represented in foothill communities, and poorly represented in desert communities.

Values for the southern class show the opposite relationship. They are poorly represented in montane communities and well represented in desert communities.

Members of the endemic class show a high degree of habitat specialization ($FI = 1.24$), and are overrepresented in relatively xeric communities at low and middle elevations. They are noticeably underrepresented in riparian communities. This may be because xeric environments tend to be more heterogeneous than mesic habitats in respect to variables other than moisture, and heterogeneous environments tend to restrict migration of specialized plant species, thus keeping them endemic.

Possible relationships between the areal extent of a distribution type and the ecological amplitude of the component species will now be explored. Table 3 gives fidelity index values and percent community composition for each of the five areal distribution classes. These show that a distribution type which covers a large area is more likely to include species with broad tolerances than a distribution type which covers a small area. The endemic and restricted classes show higher habitat specialization than the moderate class, which in turn shows a higher value than the wide class. This makes sense in light of the fact that species with broad tolerances should not only have more favorable sites available to them, but they should also be able to migrate more rapidly to occupy these sites.

An exception to this trend is exhibited by the continental + class, which contains a high proportion of transoceanic species. The community composition values for species of this class show that they are heavily concentrated in communities which provide aquatic habitat, and in fact many of these species are restricted to aquatic environments. They have probably been able to achieve wide distributions in spite of being habitat specialists by virtue of superior dispersal efficiency. It is these species which bring the index value for the Continental + group to a value which seems anomalously high.

TABLE 3. Fidelity indices, percent edaphically restricted species, and percent composition of plant communities by areal class.

	Endemic	Restricted	Moderate	Wide	Continental +
% Total Native Flora	7.8	27.5	16.8	33.0	12.8
Fidelity Index	1.24	1.25	1.00	0.83	1.01
% Edaphically Restricted Species	36.1	39.8	15.7	7.2	0
% Hot Desert Shrub	6.6	44.5	23.4	21.4	1.7
% Cold Desert Shrub	7.0	21.3	17.8	43.5	7.9
% Desert Riparian	2.9	17.0	17.3	37.5	22.7
% Foothill Woodland	10.1	20.1	21.5	40.3	4.4
% Mountain Brush	8.2	14.9	21.2	46.6	6.3
% Transition Forest	7.8	18.3	15.1	46.1	11.0
% Mountain Forest	4.7	19.5	8.9	45.3	19.5
% Mountain Riparian	2.7	13.1	5.9	44.6	32.0
% Mountain Meadow	4.6	12.1	11.2	49.5	22.4

Plants of wide but subcontinental distributions do not show this specialization, but instead are well represented in all but the Hot Desert Shrub community type. Plants of moderate distribution tend to be better represented in the lower-elevation communities. The trend continues in the group of restricted distribution, which is relatively underrepresented in all but the Hot Desert Shrub community type. This trend seems to indicate that groups of wider distribution show higher percentages in mesic types, while groups of narrower distribution show higher percentages in xeric types. This makes sense in view of the relative proportion of mesic to xeric environments in the world, on the continent, in the West, and in the intermountain-southwestern area, respectively. The values for the endemic class have been discussed above.

The importance of edaphic factors in the transition area will be examined next. Tolerance for edaphic factors, like tolerance for other environmental factors, is a matter of degree. This discussion takes into account only those species which have a very narrow edaphic requirement. Even though these make up only about 8 percent of the total flora, the implication that edaphic factors play a minor role in the transition area is not warranted. Many more species show some degree of edaphic specialization, and as noted above, distributional limits are not all or nothing propositions based on pres-

ence or absence of adaptive traits, but instead are also a matter of degree. The patterns for the sharply restricted species seem to indicate that edaphics may be more important in the transition area than might be supposed.

Table 4 shows the percentage of all species versus the percentage of edaphically restricted species occurring in each community type. Though both these values tend to decrease with an increase in altitude, edaphically restricted species drop much more sharply. In addition, this group is poorly represented in the Desert Riparian community. Clearly edaphically restricted species are much better represented in xeric than in mesic community types. This may indicate that the environment is more heterogeneous edaphically in dry than in wetter environments. Mesic soils developed on different substrates tend to be more modified and more alike than xeric soils developed on those different substrates.

A consequence of such environmental heterogeneity is that edaphically restricted species tend to belong to more restricted areal distribution types. This is because species with narrow edaphic tolerances migrate slowly through an edaphically heterogeneous area. It may also be because the substrate itself is of restricted geographic occurrence. The first and third rows of Table 3 demonstrate this relationship.

An edaphically restricted species will be able to migrate relatively rapidly in spite of low genetic heterogeneity as long as the environment is homogeneous and favorable in terms of substrate. When such a species reaches a range limit, it is probably because it has reached a point where the substrate environment suddenly becomes very heterogeneous or homogeneous and unfavorable. The favorable substrate may occur at widely spaced sites of small areal extent instead of closely spaced sites of large areal extent, or it may be completely absent from the potential area. In any case, the average minimum dispersal distance becomes prohi-

TABLE 4. Percentage of all native species and of all edaphically restricted species occurring in each plant community.

Plant Community	% Total Native Species	% Edaphically Restricted Species
Hot Desert Shrub	32.4	63.9
Cold Desert Shrub	29.5	37.3
Desert Riparian	26.0	13.3
Foothill Woodland	27.9	32.5
Mountain Brush	19.5	15.7
Transition Forest	20.5	12.1
Mountain Forest	17.8	2.4
Mountain Riparian	20.8	2.4
Mountain Meadow	10.0	1.2

bitively large, and migration slows to near zero.

Table 5 shows the substrate preferences of edaphically restricted species belonging to each of the seven directional distribution classes. The northern class contributes no edaphically restricted species. This is not surprising in view of the high preference of this group for mesic environments, which do not promote edaphic specialization.

The nondirectional class contributes only one limestone-restricted and one sandstone-restricted species, and as a group is markedly underrepresented. The southern class and the Great Basin class are also slightly underrepresented and contribute only a handful of the edaphically restricted species. This means that most of these species must be contributed by the remaining three classes.

Over a quarter of the species are contributed by the Mojave class, but these are distributed very unevenly among the substrates. Mojave species constitute almost two-thirds of the limestone-restricted class, about one-fourth of the sand-restricted class, and less than 10 percent to the remaining classes.

The Colorado Plateau class accounts for almost a third of the total. But, in contrast to the Mojave class, none of these are limestone-restricted. Instead they make up almost two-fifths of the sandstone-restricted species, one-fifth of the clay-restricted species, and about two-thirds of the sand-restricted species.

The endemic class accounts for the remaining third of the total. This class contributes the only volcanic-restricted species, about three-quarters of the clay-restricted species, and two-thirds of the sandstone-restricted species. None of the endemics are sand restricted.

Over 90 percent of the edaphically restricted species are range-terminating. The role of substrate specialization as a factor in range-termination seems clear. Limestone-restricted species appear to migrate rapidly across the southern Basin and Range Province, but their rate of migration nears zero when they encounter the sandstones and shales of the Colorado Plateau. Conversely, sandstone- and clay-restricted species seem to migrate rapidly across the Colorado Plateau, but their rate of migration nears zero when they encounter the high-carbonate soils of the Basin and Range Province. Sand is a substrate which is widespread, especially in the Colorado Plateau Province; thus sand-restricted species do not tend to be endemics. But there is sand in the Mojave Desert; thus some sand-restricted species enter the county via the Mojave. These may be prevented from migrating further north by other than edaphic factors.

SUMMARY

The data show that the high proportion of range-terminating species in the county flora is correlated with the abrupt shifts

TABLE 5. Edaphically restricted species by substrate and directional class.

Directional Class	% Total Native Flora	% Edaphically Restricted Group	% Volcanic-Restricted Species	% Sand-Restricted Species	% Sandstone-Restricted Species	% Limestone-Restricted Species	% Clay-Restricted Species
Endemic	7.8	36.1	100.0	0	62.5	15.8	69.6
Nondirectional	25.5	2.4	0	0	0	10.6	0
Mojave	17.6	24.0	0	25.0	0	63.2	8.7
Colorado Plateau	14.3	28.9	0	54.2	37.5	0	21.7
Great Basin	6.6	3.6	0	8.3	0	5.2	0
Northern	20.5	0	0	0	0	0	0
Southern	5.5	3.6	0	8.3	0	5.2	0
Anamalous	2.2	1.2	0	4.2	0	0	0
Total Species	100.0	100.0	100.0	100.0	100.0	100.0	100.0
% Total Edaphically Restricted Species	—	—	1.2	28.9	19.3	22.9	27.7

along environmental gradients oriented in north-south and in east-west directions. The north-south gradient is primarily climatic, while the east-west gradient is both climatic and edaphic.

Species with narrower tolerances are shown to be more sensitive to these abrupt environmental shifts. It is also shown that some of the range-terminating species have the capacity to migrate beyond the transition zone under present conditions, but that differences in relative migration rates give their distributional limits within the county a quasi-stable aspect.

CONCLUSION

Just about anything is statistically possible in biogeography. This makes it dangerous to conclude that any species has a migration rate of zero. It is possible for a propagule to be dispersed to a tiny enclave of favorable environment in the midst of a vast area of homogeneous and unfavorable environment. And it is possible that the very rare propagule which has tolerance characters near an extreme for the species will be dispersed to a site for which it is pre-adapted. These events may be very unlikely, but they are possible. They may result in some of the seemingly aberrant "dots" often seen on species distribution maps.

Instead of considering only two possibilities, those species which are environment-limited in their current distribution pattern and those which are not, it seems far better to consider these two possibilities as extremes on a continuum. This involves recognition of the interplay among a complex series of factors which interact to produce the probability that a species will be able to migrate at a given rate under a given set of conditions. These concepts may prove difficult to tie down, but it is hoped the ideas presented here will facilitate the process—if they only begin to sharpen the focus on this complex and interesting problem.

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THE THEORY OF INSULAR BIOGEOGRAPHY AND THE DISTRIBUTION OF BOREAL BIRDS AND MAMMALS

James H. Brown¹

ABSTRACT.—The present paper compares the distribution of boreal birds and mammals among the isolated mountain ranges of the Great Basin and relates those patterns to the developing theory of insular biogeography. The results indicate that the distribution of permanent resident bird species represents an approximate equilibrium between contemporary rates of colonization and extinction. A shallow slope of the species-area curve ($Z = 0.165$), no significant reduction in numbers of species as a function of insular isolation (distance to nearest continent), and a strong dependence of species diversity on habitat diversity all suggest that immigration rates of boreal birds are sufficiently high to maintain populations on almost all islands where there are appropriate habitats. In contrast, the insular faunas of boreal mammals represent relictual populations that receive no significant contemporary immigration. The insular mammal faunas have been derived by extinction from a set of species that colonized the islands when habitat bridges connected them to the continents in the late Pleistocene. A relatively steep species-area curve ($Z = 0.326$), no effect of isolation on species diversity, and the absence of appropriate species from large areas of apparently suitable habitat all support this conclusion. Measures of habitat diversity that are closely correlated with bird species diversity do not account for much of the variation in number of mammal species among islands. Insular area is the single variable that accounts for most of the variability in both bird and mammal species diversity; this supports the approach of using standard parameters such as area in comparative empirical analyses and general biogeographic theory. The results of this study suggest that extremes of vagility among taxa and a recent history of paleoclimatic and geological changes make it unlikely that equilibrium distributions, of the sort MacArthur and Wilson (1967) propose for the biotas of oceanic islands, are characteristic of the insular distributions of terrestrial and freshwater vertebrates of western North America.

Biogeography is an old science that has made recent advances by assimilating new concepts and data. Within the last two decades information on continental drift, paleoclimatology, and ancient sea levels has revolutionized our understanding of historical events and their effects on plant and animal distribution. During the same period, ecologists and evolutionary biologists have learned much about the processes of population growth, dispersal, extinction, speciation, and interspecific interactions which are the mechanisms that determine distribution. Biogeography appears to be entering an exciting new period in which the voluminous data acquired by systematists and descriptive biogeographers can be interpreted in terms of recently understood historical events and ecological processes to

draw quantitative relationships and derive general principles.

With the publication of their equilibrium model of insular distribution, MacArthur and Wilson (1963, 1967) contributed not only a new theory but also a new approach to biogeography. Prior to their work, most biogeographic research had consisted of describing the distributions of particular taxa and producing ad hoc, historical explanations. MacArthur and Wilson advocated a quantitative approach designed to build and test general models based on ecological processes. The specific model that they proposed suggests that the number of species inhabiting an island represents an equilibrium between opposing rates of extinction and colonization, and that these processes are functions of the size of an island and its

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distance from a source of colonists, respectively.

MacArthur and Wilson's choice of islands for their revolutionary approach to biogeography was not a fortuitous one. Ever since the pioneering work of Darwin and Wallace, islands have played a preeminent role in the development of the science. It is difficult to do experiments in biogeography, but islands and insular habitats represent natural experiments; they are small, replicated systems among which species and environmental parameters are distributed in different combinations. Often particular taxa are distributed among insular habitats in patterns that imply the operation of general mechanisms of dispersal, extinction, and interspecific interaction. The last decade has seen several attempts to test the model of MacArthur and Wilson, using a variety of organisms that inhabit both true islands and analogous isolated habitats (e.g., Barbour and Brown 1974, Brown 1971, Brown and Kodric-Brown in review, Culver 1970, Culver et al. 1973, Diamond 1969, 1970a, 1971, Johnson 1975, Harper et al. this symposium, Schoener 1974, Seifert 1975, Simberloff 1974, Simberloff and Wilson 1970, Simpson 1974, Terborgh 1973, Vuilleumier 1970, 1973). Not all of these studies have supported the model, but the exceptions have contributed importantly to our understanding of the patterns of insular distribution and the historical events and ecological processes that produce them.

Analysis of the distribution of vertebrates among isolated habitats in the Intermountain Region of western North America has contributed significantly to the development and testing of biogeographic theory. The dedicated field work of several generations of systematists has documented in detail the species distributions of most vertebrate groups (e.g., for fishes Miller 1948, Hubbs and Miller 1948, Hubbs et al. 1974, Smith, this symposium; for birds Behle 1943, 1955, 1958, this symposium, Grinnell and Miller 1944, Johnson 1965, 1970, 1973, 1974, 1975, Linsdale 1936, Miller 1935,

1946, Miller and Russell 1956, Van Rossem 1936; for mammals Durrant 1952, Durrant et al. 1955, Grinnell 1933, Hall 1946). The paleoclimatic history of the region also is becoming increasingly well understood (e.g., Hubbs and Miller 1948, Martin and Mehringer 1965, Smith this symposium, Wells and Berger 1967, Wells and Jorgensen 1964). This excellent data base has been used in quantitative analyses of the insular distributions of lacustrine fishes (Barbour and Brown 1974) and montane birds (Johnson 1975) and mammals (Brown 1971). Much more work remains to be done. Some of the most interesting contributions can be expected when additional kinds of organisms and insular habitats are studied, so that it is possible to make comparisons among taxa which differ in ecological requirements and dispersal abilities, and among habitats that differ in environmental parameters and history of isolation.

The present paper discusses the distribution of boreal birds and mammals among isolated mountain ranges in the Great Basin in relation to the theory of insular biogeography. It attempts to relate distributional patterns to mechanisms of dispersal and extinction and to differentiate relictual patterns that are the legacy of historical events from equilibrial ones that can be attributed to contemporary ecological processes. The paper tries to develop a general conceptual basis for analyzing and predicting insular distributions. It first discusses the current state of insular biogeographic theory and then utilizes empirical data on the distribution of boreal birds and mammals to test the theory and search for general mechanisms.

THE THEORY OF INSULAR BIOGEOGRAPHY

Colonization, extinction, and speciation are the primary processes that determine the composition of insular biotas. An island can be defined as a patch of suitable habitat surrounded by unfavorable environment that limits the dispersal of individuals. New spe-

cies colonize an island either by dispersing across the habitat barriers or by immigrating sometime when the barriers were temporarily absent. Speciation entirely within an island potentially is another source of new species, but there is no evidence that this process has contributed significantly to the diversity of boreal birds and mammals in the Great Basin region. Extinction, which may be caused by a variety of factors that reduce population size, eliminates species and reduces insular diversity. The composition of an insular biota is determined by the interaction of these origination and extinction processes.

MacArthur and Wilson (1963, 1967) developed a simple, general model of insular biogeography that represents the number of species inhabiting an island as an equilibrium between contemporary rates of colonization and extinction (Fig. 1). Their model makes the colonization rate a decreasing function of distance to a source of dispersing species (usually the nearest continent) and extinction rate a decreasing func-

tion of island size. The model predicts: first, that relatively constant insular species diversity is maintained by the continual turnover (extinction and colonization) of individual species; second, that the equilibrium number of species is positively correlated with island size and negatively correlated with distance to the source of potential colonists; and third, that the equilibrium turnover rate is inversely related to both island size and distance to a source of species. Although the MacArthur-Wilson model was designed specifically to account for the diversity of organisms on oceanic islands, it has proven a useful heuristic device for analyzing many kinds of insular distributions because it deals with general processes and makes robust, testable predictions.

As the MacArthur-Wilson model has been tested using a variety of taxa distributed among both oceanic islands and several kinds of insular habitats (see references cited above), it has become increasingly clear that in its present form it is inadequate to account for many empirical ex-

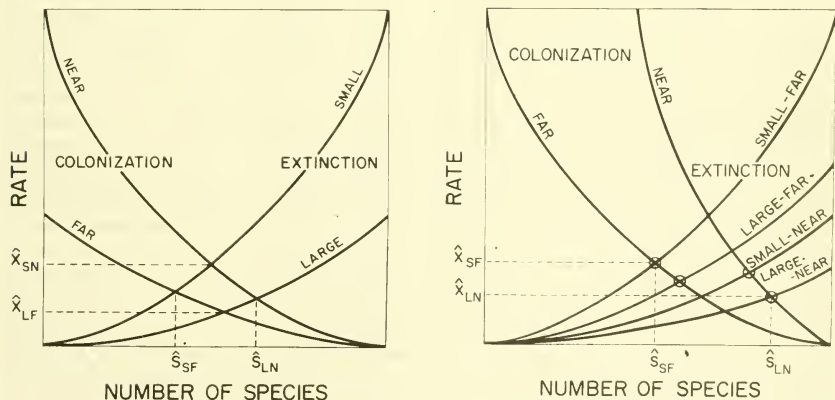


Fig. 1. Two models of equilibrium insular biogeography. Left, the MacArthur-Wilson model, which portrays extinction and colonization rates as functions of island size and isolation respectively. Right, a modification of the MacArthur-Wilson model by Brown and Kodric-Brown (1977), which incorporates the effect of insular isolation on extinction rate. In both models intersections of the curves can be extrapolated to the abscissa and ordinate to give equilibrial numbers of species (\hat{S}) and turnover rates (\hat{X}), respectively. Note that the two models predict the same relative order of numbers of species but different orders of turnover rates with respect to island size and isolation.

amples. Two major problems have arisen in attempts to use the model to account for empirical patterns of animal and plant distribution. First, in some insular habitats, historical episodes of immigration, speciation, and extinction have produced numbers of species that are significantly greater or less than the equilibrium number expected on the basis of contemporary rates of colonization and extinction (Barbour and Brown 1974, Brown 1971, Culver et al. 1973, Diamond 1970). Such historically determined distributions should be particularly common in organisms that are poor dispersers (such as the small, nonflying vertebrates) and in geographic areas (such as western North America) where paleoclimatic and geological changes have drastically altered the barriers that currently isolate insular habitats. Second, it has proven difficult to test the MacArthur-Wilson model's critical predictions about insular turnover. Although it is relatively easy to census accurately the biota of an island, it is much more difficult to assess the natural turnover rate. As a result, most of the purported measures of insular turnovers have been criticized (see Diamond 1969, 1971, Terborgh 1973, Lynch and Johnson 1974, Simberloff 1974), and the critical predictions of how turnover rate varies with island size and isolation remain untested. Recently, Brown and Kodric-Brown (1977) obtained empirical evidence that insular extinction rates may be strongly dependent on the distance of an island from a source of colonists, rather than on island size alone as MacArthur and Wilson suggest. Areas that are sources of colonizing species often also may be sources of immigrant individuals of species already present on the island; the arrival of these immigrants may refute the probability that insular populations go extinct. We predicted that, for many islands, species turnover rates are lower for islands near sources of dispersing species than for more isolated ones. Although this is the opposite of the pattern predicted by the MacArthur-Wilson model, the model can easily be modified to in-

corporate this influence of immigration on extinction rate (Fig. 1).

Neither of these problems detracts from the utility of MacArthur and Wilson's model as a heuristic device or the value of their approach. Their work did much to stimulate biogeographers to develop precise hypotheses and test them with appropriately analyzed quantitative data. Gradually a conceptual understanding of insular biogeography is emerging that may not be as simple and elegant as the MacArthur-Wilson model, but it is hoped it will be more realistic. In the following sections, I hope to use the distribution of boreal birds and mammals among isolated mountain ranges in the Great Basin to illustrate this theoretical approach and some of the resulting concepts.

MONTANE ISLANDS

The mountain ranges of the Great Basin are islands of coniferous forest and associated mesic habitats in a sea of desert. The Great Basin is a vast interior drainage that lies between two montane continents, the central mountains of Utah (a part of the Rocky Mountains) on the east and the Sierra Nevada on the west (Fig. 2). Most of this area consists of broad arid valleys, which lie at an elevation of approximately 5000 feet and are sparsely covered with a vegetation dominated by low woody shrubs of the genera *Artemisia*, *Chrysothamnus*, and *Atriplex*. Between the valleys are a series of mountain ranges oriented in a north-south direction. Many of these rise to over 10,000 feet; on their lower slopes they are covered with juniper-pinyon woodland and at higher elevations there are forests of mixed conifers, stands of aspens, and sometimes wet meadows and permanent streams.

The present analysis is based on 19 islands for which the boreal mammal fauna is adequately known; lists of boreal bird species are available for 13 of these. Islands were defined by operational criteria applied to topographic maps (U.S. Geological Sur-

vey maps of the states: scale 1:500,000). A montane island was considered to be a mountain range that contains at least one peak higher than 9800 feet and is separated from other highland areas by a valley at least 5 miles across below an elevation of 7500 feet. This altitude represents the approximate lower boundary of juniper-pinyon woodland. For each island, area above 7500 feet elevation, distance to nearest continent (Sierra Nevada or central mountains of Utah), and elevation of highest peak were determined from topographic maps (Table 1). For 13 islands ornithologists (Johnson 1975, Behle, this symposium) have quantified the diversity of habitats available to boreal birds. This habitat diversity score incorporates the number of coniferous tree

species and the presence of riparian woodland, wet meadow, and aquatic habitats (see Johnson 1975 for details). Since West (this symposium) has shown that juniper-pinyon woodland is absent or poorly developed in the northern Great Basin, the islands selected for this analysis lie south of the Humboldt River and Great Salt Lake to insure that they have somewhat comparable habitats.

BOREAL BIRDS AND MAMMALS

For the bird and mammal species that are restricted to juniper-pinyon woodland and more mesic habitats of higher elevations, the mountains of the Great Basin are truly islands. Their boreal avian and mam-

TABLE 1. Data for the boreal habitats used in the present analysis.

Great Basin Montane "Islands"	Area above 7,500 feet (sq. miles)	Highest peak (feet)	Nearest continent (miles)	Habitat diversity score ¹	Permanent resident bird species ²	Small Boreal mammal species ³
1. White-Inyo	738	14,242	10	11	8	11
2. Panamint	47	11,045	52	3	5	3
3. Desatoya	83	9,814	83	2	4	7
4. Toiyabe-Shoshone	684	11,788	110	7	6	13
5. Toquima-Monitor	1,178	11,949	114	—	—	10
6. Roberts Creek	52	10,133	216	—	—	4
7. Diamond	159	10,614	190	—	—	4
8. Ruby	364	11,387	173	9	6	12
9. Spring	125	11,918	125	7	6	6
10. Sheep	54	9,912	86	5	5	3
11. Grant-Quinn Canyon	150	11,298	138	9	5	5
12. White Pine	262	11,188	150	—	—	7
13. Schell Creek-Egan	1,020	11,883	114	—	—	8
14. Spruce-South Pequop	49	10,262	156	4	4	4
15. Snake	417	13,063	89	14	9	10
16. Deep Creek	223	12,101	104	11	7	8
17. Pilot	12	10,704	114	—	—	3
18. Stansbury	56	11,031	39	8	6	6
19. Oquirrh	82	10,626	19	9	6	6
Sierra Nevada Mainland						
20. Carson	284	10,788	0	17	13	22
21. Yosemite	828	13,090	0	18	15	23
Rocky Mountain Mainland						
22. Paunsaugunt-Aquarius	1,008	11,124	0	14	13	16
23. Uinta	1,536	13,498	0	15	14	21

¹From Johnson (1975) and Behle (this symposium).

²See Appendix 1 for documentation.

³See Appendix 2 for documentation.

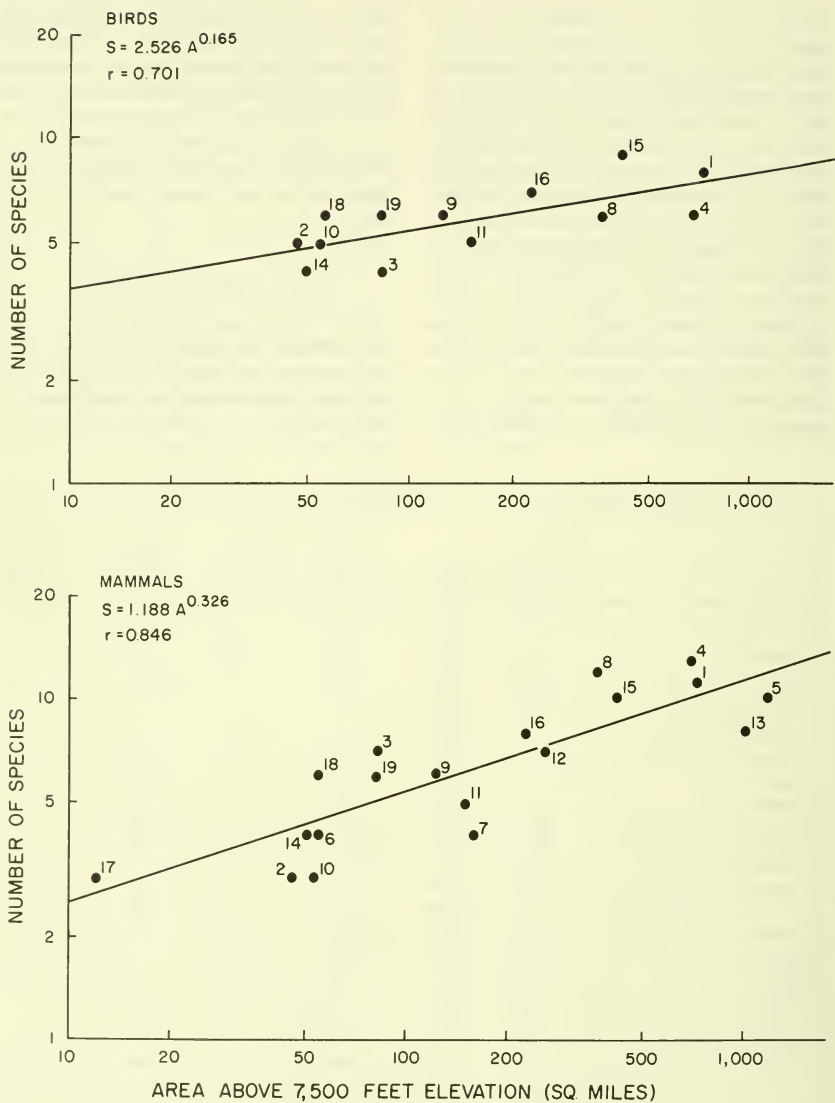


Fig. 2. Map of the Great Basin region of western North America showing the location of the isolated mountain ranges used in the present analysis. Numbers refer to individual montane islands and continental sample areas listed in Table 1. Note that islands of varying size and isolation lie in the "sea" of desert habitat between the central mountains of Utah on the east and the Sierra Nevada of California on the west.

malian faunas are depauperate subsamples of the Sierra Nevada and Rocky Mountain faunas. All of the bird and mammal species that inhabit the isolated peaks are broadly distributed on one or (more frequently) both of the continental ranges to the east and west (see appendix and references cited there), but a significant proportion of the continental species are not present on any particular island and some are absent from all islands. The continental mountain ranges clearly are the source of the insular boreal faunas, and the distribution of species on the islands is the result of their abilities to colonize and avoid subsequent extinction.

The definition of boreal bird and mammal species is somewhat arbitrary, and the lists of knowledgeable specialists often do not agree precisely (e.g., compare the lists of boreal bird species of Johnson 1975, and Behle this symposium). I have followed Johnson's rather conservative designation of boreal bird species (for a list of these species and their distribution see Appendix 1). I have restricted my analysis to those species that he terms (again conservatively) "permanent resident Boreal species," because I wanted to include in my comparison with mammals only those species that maintain sedentary populations throughout the year. This eliminates from the analysis the large number of bird species that breed on the montane islands but are likely to migrate or disperse long distances between successive breeding seasons. The definition of boreal mammal species includes those that inhabit juniper-pinyon woodland or habitats of higher elevation, but not the desert habitats of the Great Basin. I have excluded from the analysis large carnivores and ungulates because their distributions have been drastically altered by human activity and their original ranges and habitat requirements are poorly known. Also I have ignored bats, because their distributions are incompletely documented and they, like the migratory birds, probably are not permanent residents of the islands. The list of boreal mammal species (Appendix 2)

is similar to that in Brown (1971), but it differs in some details because I have used slightly different criteria for designating boreal species and I have included a few more records of occurrence. The resulting lists of boreal bird and mammals contain species of generally similar body sizes and habitat requirements, although there are approximately 50 percent more mammal than bird species on both the large islands and the continents.

SPECIES—AREA RELATIONSHIPS

The number of species (S) inhabiting an island usually is positively correlated with insular area (A); this relationship takes the form $S = CA^Z$, where the values of the constant (C) and slope (Z) depend on the characteristics of the specific taxon and group of islands under consideration (MacArthur and Wilson 1967, Preston 1962). The slope of this relationship can indicate the relative importance of extinction and origination processes in determining the diversity of insular biotas. (Barbour and Brown 1974, Brown 1971, MacArthur and Wilson 1967). Low slopes, $Z < 0.20$, tend to characterize samples of different areas within a continent, and the Z -value varies with environmental heterogeneity (Harner and Harper, 1977). Islands usually have higher Z -values; when the insular biota represents an approximate equilibrium between rates of colonization and extinction, Z -values tend to lie in the range 0.20-0.35. When there is no contemporary colonization to oppose extinction, islands tend to have even higher Z -values, often > 0.40 . The reason for this pattern is straightforward. On continents small sample areas contain a significant proportion of rare species. If these habitats were isolated and no immigration were permitted, rare species would go extinct rapidly on small islands and much more slowly on large ones, producing a much steeper species-area curve. Islands in equilibrium, where a significant rate of colonization opposes extinction, represent an intermediate

situation; species that go extinct on small islands tend to be replaced by colonists, but not at a sufficient rate to produce diversity comparable to that on continents. There can be exceptions to this pattern. For example, if only a small subsample of the continental biota is able to colonize a group of islands, the Z-value may be lower than expected because large islands will not acquire as many species as they can support (Barbour and Brown 1974).

This conceptual framework can be used to compare the species-area curves for the boreal birds and mammals. In my earlier analysis (Brown 1971), I argued that boreal mammals reached all of the islands during periods of climatic change in the late Pleistocene; since then there have been extinctions but no colonizations. This con-

clusion can be tested using a somewhat different data set for mammals and comparing the mammalian and avian distributions. If birds are better dispersers and are currently crossing the desert valleys to colonize the isolated peaks, then they should have a significantly lower Z-value than mammals. This is the case. The number of species of both birds and mammals is correlated significantly with area (Fig. 3, Tables 2 and 3). The Z-value for birds, 0.165, is even lower than that obtained for most insular biotas that are presumed to be in equilibrium and approximates values for continental samples. The Z-value for mammals, 0.326, is less than I obtained in my earlier analysis, $Z = 0.428$, and lies in the upper range of those observed for the biotas of true islands (MacArthur and Wilson 1967). Thus species-area

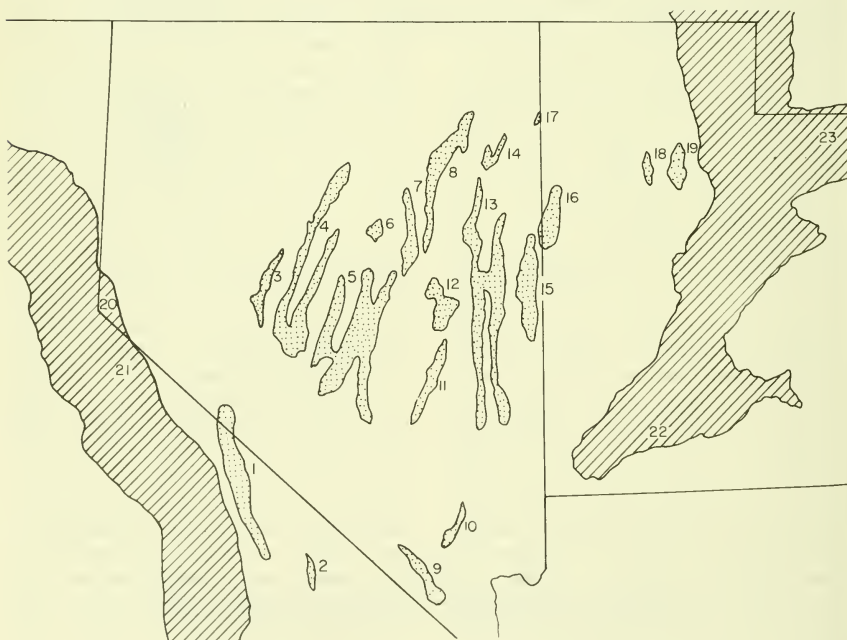


Fig. 3. The relationship of insular area to the number of permanent resident boreal bird species (above) and the number of small boreal mammal species (below). Note that the slope of the least squares regression line of the species-area curve for birds is much less steep than that for mammals. The equations for the fitted regressions and the correlation coefficients (r) are indicated.

curves for the boreal birds and mammals conform qualitatively to theoretical predictions, but they differ slightly from the quantitative Z-values that might be expected if the avian distribution represents an equilibrium between contemporary colonization and extinction, and the insular mammalian populations are Pleistocene relicts that do not disperse across the desert valleys.

These slight deviations from expected Z-values are not difficult to explain. The low Z-value for birds suggests that the isolation of the montane islands may not be a significant barrier to avian colonization. The facts that a) approximately 80 percent of the variation in insular bird species diversity can be accounted for by the combined effects of area and elevation (Table 2) or by habitat diversity (Table 3), and b) there appears to be no impoverishment of species numbers resulting from isolation by distance to the

nearest continent (Table 2, and see next section) suggest that colonization rates are high and there is little if any effect of insular isolation. This is consistent with Johnson's (1975) conclusion that the diversity of boreal birds is attributable primarily to habitat; the impoverishment of the insular avifaunas is the result of reduced habitat diversity on the isolated peaks and not to any significant extent to low colonization rates. It should be noted that it is not necessary to infer from this that the desert valleys do not inhibit dispersal, only that colonization rates remain sufficiently high that boreal species which maintain breeding populations on the islands rarely go extinct and, if they do, they recolonize rapidly.

The fact that the Z-value for mammals also is slightly lower than predicted has a different explanation. As I shall show in the next section, the mammals that have colo-

TABLE 2. Stepwise multiple regression of the influence of three variables on the number of species of boreal birds and mammals inhabiting montane islands in the Great Basin.

BIRDS				
Variable ¹	Order entered in equation	Contribution to R ²	F-value	Significance level
Area	1	0.4915	10.633	0.008
Highest peak	2	0.2836	12.607	0.005
Nearest continent	3	0.0051	0.201	0.658

MAMMALS				
Variable ¹	Order entered in equation	Contribution to R ²	F-value	Significance level
Area	1	0.716	42.957	<0.001
Highest peak	2	0.005	0.271	0.610
Nearest continent	3	0.010	0.559	0.466

¹Data are log-transformed data from Table 1.

TABLE 3. Correlation coefficients (r) between variables for the 13 montane islands for which all data are available. Upper right matrix is log-transformed data; lower left matrix is computed with untransformed data. Note that number of bird and mammal species are not closely correlated with the same variables.

	Area	Highest peak	Nearest continent	Habitat diversity	Bird species	Mammal species
Area	—	0.795	-0.079	0.623	0.701	0.891
Highest peak	0.778	—	-0.334	0.722	0.869	0.523
Nearest continent	-0.083	-0.224	—	-0.176	-0.367	-0.070
Habitat diversity	0.524	0.760	-0.102	—	0.851	0.539
Bird species	0.637	0.872	-0.310	0.898	—	0.611
Mammal species	0.876	0.817	0.090	0.542	0.592	—

nized the montane islands are those species of the continental fauna that occur at relatively low elevations within the boreal zone; species restricted to high elevations are absent from all of the isolated mountain ranges. The large islands, which also tend to have the highest peaks (Table 3), have extensive areas of mixed coniferous forest, wet meadow, and other high altitude habitats. Even with post-Pleistocene extinctions these mountains would be expected to support some of the mammal species characteristic of these habitats on the continental ranges. Thus, if the islands had an unbiased sample of the boreal mammal fauna, the larger islands should have more species than they do and the species-area curve would be steeper. In my 1971 paper, I reported a higher Z-value than obtained here. The reason is that I included in the present analysis some marginally boreal species (*Eutamias dorsalis*, *E. panamintinus*, and *Sylvilagus nuttalli*) that are characteristic of juniper-pinyon woodland and are present on most of the montane islands. This had the effect of adding an approximately constant number of species to the fauna of all islands, and thus lowering the slope of the exponential species-area relationship. This is the same effect that is produced by the disproportionate representation of low elevation species in the insular faunas relative to continental faunas because of differential colonization in the past.

ISOLATION AND PALEOCLIMATIC HISTORY

It is a common observation of insular biogeography that remote islands support fewer species than islands of comparable size and habitat diversity that are nearer to a continent (see MacArthur and Wilson 1967 and included references). This pattern is attributed to the limited ability of organisms to disperse so that the rate of immigration to an island declines with increasing isolation. In the present analysis, neither birds nor mammals demonstrate such a negative relationship between number of

species and distance to the nearest continent (Tables 2 and 3). For mammals, this result is consistent with my 1971 analysis and conclusion that there is virtually no contemporary immigration to the isolated mountains because the desert valleys constitute almost absolute barriers to dispersal. The islands were colonized in the Pleistocene when periodic climate changes resulted in shifts in the altitudinal limits of the boreal vegetation. Data from plant macrofossils in woodrat middens suggest that, as recently as 8,000 to 12,000 years ago, periods of cooler, wetter climate enabled juniper-pinyon woodland to flourish at least 2,000 feet (600 m) below its present lower elevational limit (Wells and Berger 1967, Wells and Jorgensen 1964). This was sufficient to make juniper-pinyon and associated meadow and riparian habitats contiguous across virtually all of the Great Basin, and to enable the boreal mammals characteristic of these habitats to colonize all of the isolated mountain ranges. With the return of hotter, drier conditions, these "habitat bridges" connecting the islands to the continental ranges were eliminated and the insular mammalian faunas have been derived from the widespread Pleistocene fauna by independent extinctions on each island.

Several lines of evidence are consistent with this interpretation. 1) The relatively steep species-area curve (Fig. 3) suggests that extinction has played a major role in determining mammalian diversity. This is supported by the discovery of late Pleistocene fossils of at least one boreal species (*Marmota flaviventris*) from an island (Spring Range) where it no longer occurs (Wells and Jorgensen 1964). 2) The lack of any correlation between number of mammal species and distance to nearest mainland (Tables 2 and 3) or any other likely measure of insular isolation (Brown 1971) suggests that there is no contemporary immigration to the islands. 3) All of the species known from the islands are found in juniper-pinyon or other habitats of comparable elevation. It is possible to account

for the presence of the entire insular fauna in terms of colonization across habitat bridges that were known to have existed in the late Pleistocene. 4) All of the species of boreal mammals that are restricted to mixed coniferous forest or habitats of higher elevation on the continental ranges are absent from all of the montane islands, even though large areas of apparently suitable habitat are present on some of the larger islands. These species include *Martes americana*, *Aplodontia rufa*, *Eutamias alpinus*, *E. townsendi*, *E. speciosus*, *Tamiasciurus hudsonicus*, *T. douglasi*, *Glaucomys sabrinus*, *Phenacomys intermedius*, *Clethrionomys gapperi* and *Lepus americanus*. Paleobotanical evidence indicates that the habitats of these species were not connected across the Great Basin during the late Pleistocene. This is further evidence that small terrestrial mammals usually are unable to cross habitat barriers only a few miles in extent and thus colonize isolated habitats only when bridges of appropriate habitat provide direct access (Brown 1971, 1973).

The explanation for the lack of correlation between number of species and distance to nearest continent in birds appears to be the opposite of that in mammals: birds are such good dispersers that they have colonized virtually all islands with suitable habitat regardless of their isolation. Both Johnson (1975) and Behle (this symposium) report a negative relationship between their measure of insular isolation (cumulative width of desert barriers) and number of permanent resident bird species, but both authors included continental sample areas in their analyses. The apparent effect of isolation in their analyses can be attributed largely to the fact that a significantly greater number of species inhabit continental sites than occur on the islands; there is little or no effect of isolation by distance when only islands are considered (see Fig. 2 of Johnson 1975). This is consistent with my own analysis of Johnson's and Behle's data. There is an insignificant negative correlation between number of

bird species and distance to nearest continent (Table 3), and the distance variable does not contribute significantly to accounting for number of bird species using multiple regression analysis (Table 2). It remains to explain the difference in species diversity between the continents and islands. Some of those species present on the continents but absent from most of the islands may be limited in their distributions by their sedentary natures or their aversion to crossing inhospitable desert terrain. However, many of these species such as *Lagopus leucurus*, *Dryocopus pileatus*, and *Perisoreus canadensis*, have specialized habitat requirements and low population densities. Their habitats are totally lacking from many of the islands, and, even where they are present, they often consist of small patches obviously inadequate to support sustained populations. Two other sources of evidence suggest that rates of contemporary immigration by most boreal bird species are sufficiently high to keep the habitats present on the islands filled with an appropriate complement of species. First, such boreal bird species as *Picoides tridactylus* and *Cyanositta stelleri*, which are restricted to high elevation, well-developed coniferous forests, are present on the islands. Since the habitats of these species have not been connected by bridges to the continental ranges during the Pleistocene, it must be inferred that at least these species are able to colonize across significant barriers of unsuitable habitat. Second, vagrant individuals of some boreal species (e.g., *Cyanositta stelleri* and *Cinclus mexicanus*) infrequently are reported significant distances from breeding populations (Johnson 1975, B. Bundick, pers comm.). This evidence indicates that even relatively sedentary permanent resident boreal birds are much more vagile than small boreal mammals.

DETERMINANTS OF SPECIES DIVERSITY AND COMPOSITION

Differences in dispersal account in large part for differences in the species-area rela-

tionships between birds and mammals and in faunal composition between insular and continental mountain ranges (at least for mammals), but the considerable variation in species diversity among the insular bird and mammal faunas must be attributed primarily to ecological characteristics of the islands. Although a common set of both bird and mammal species has had the opportunity to colonize virtually all islands, the isolated mountain ranges support different numbers and kinds of species. Species diversity of both birds and mammals is closely correlated with insular area, but area is only a correlate of factors such as the quantity and diversity of habitat and food resources that ultimately determine species diversity. Power (1972) and Johnson (1975) have shown for birds that someone familiar with a group of organisms can devise quantitative measures of habitat diversity that account for significantly more of the variance in insular species diversity than area. This approach has great utility for elucidating the environmental factors that influence the diversity and distribution of particular taxa, but it may not be useful for developing general biogeographic or ecological theory.

There are two arguments in favor of basing biogeographic theory on simple, standard parameters such as insular area. The first is practical. Parameters such as area, elevation (another correlate of habitat diversity), and distance to the nearest continent are easy to determine from maps. By obtaining these measurements and species lists from the literature, it is possible to describe clear patterns of plant and animal distribution without doing all the original fieldwork required to quantify accurately more direct environmental variables. Much of the recent synthetic work in insular biogeography has been done this way, and even those authors that have attempted to quantify variables such as habitat diversity often have used data available from the literature or topographic maps (e.g., Power 1972, Johnson 1975). The second argument is that area

may be the best parameter for constructing general theory that can be applied to diverse taxa and various kinds of islands. In the development of theory some sacrifice of precise explanation of specific cases usually must be made in order to obtain a desirable degree of generality. It is questionable whether it would be practical or profitable to base biogeographic theory on organism-specific parameters such as habitat diversity, food availability, or carrying capacity. Certainly at present we have no accepted, standardized techniques for measuring these variables in the field that are suitable for a variety of taxa and habitats.

Some test of the merit of this approach can be made by comparing the correlates of species diversity for boreal birds and mammals. Johnson (1975) developed a quantitative "habitat diversity score" that accounted for most of the variability in the number of boreal bird species in his analysis. This appears to measure accurately the requirements of boreal birds in western North America, because Behle (this symposium) tested it and obtained gratifyingly similar results. Since boreal mammals utilize the same forest, meadow, and freshwater habitats as boreal birds, it would be encouraging if Johnson's habitat diversity score accounted for similarly large proportions of the variability in insular species diversity for both taxa. Unfortunately this is not the case (Table 2). The number of boreal bird and mammal species inhabiting the same islands are not very closely correlated ($r^2 \leq 0.37$); whereas 81 percent of the variability in bird species diversity can be attributed to habitat diversity score, the comparable figure for mammals is only 29 percent. Area is by far the best correlate of species diversity for both birds and mammals. When the appropriate log-transformed data are used, area accounts for 49 and 79 percent of the variability in bird and mammal species numbers, respectively (Table 3). Interestingly, elevation of highest peak (another correlate of habitat diversity readily obtainable from topographic maps) and area taken

together in multiple regression analysis (Table 2) account for almost as much variability in bird species diversity ($r^2 = 0.76$) as the habitat diversity score ($r^2 = 0.81$).

Two explanations can be offered for the lack of good correlation between Johnson's habitat diversity score and mammalian species diversity. First, the habitat diversity score is highly dependent on the species diversity of coniferous trees. Particular tree species and forest types probably are important to the boreal birds, but they are much less likely to influence the diversity of boreal mammals. As I have shown, boreal mammals that depend on the well-developed coniferous forests of high elevations have been unable to colonize any of the islands, and those mammals that have colonized, if they require conifers at all, are primarily species of the juniper-pinyon woodlands that are well developed on almost all of the islands. Second, Johnson's habitat diversity score is based primarily on the presence or absence of particular tree species or habitat types. This qualitative approach appears to work well for birds, because they have sufficiently high immigration rates to maintain populations on almost all islands where suitable habitats are present. In contrast, mammals, which have had to maintain insular populations for thousands of years in the absence of any significant immigration, may be much more dependent on the quantity of boreal habitats (particularly those characteristic of low elevations that were connected in the Pleistocene) which may be more closely correlated with insular area than with Johnson's more qualitative index. Whether one or both of these nonexclusive explanations turn out to be correct, it is clear that different factors determine the diversity of insular species of birds and mammals. These results suggest that parameters such as area, even though their effects are indirect and imprecise, may be the variables best suited for constructing and testing general biogeographic theory.

However, specific factors that influence the insular species diversity and composition

of particular taxa can contribute to theory by providing information on the mechanisms and effects of the underlying processes of colonization and extinction. The great importance of habitat in determining insular bird species diversity, coupled with a low slope of the species-area curve and the lack of any significant effect of isolation by distance, suggests that boreal birds are able to disperse at a sufficient rate to maintain populations on most islands with suitable habitats. The distribution of boreal mammals presents a dramatic contrast. Mammal species are absent from many islands that have suitable habitats, either because they have never colonized or because they have gone extinct since the last episode of Pleistocene colonization. The interacting effects of habitat requirements and paleoclimatic changes in determining the set of species that colonized the islands already have been discussed. Of equal interest are the factors that have resulted in extinctions among the original colonists to produce the present insular faunas.

The mammalian faunas of the montane islands have been derived by extinction from a common set of 14 functional species that were widely distributed across the Great Basin during the late Pleistocene when their habitats were connected by bridges to the continental mountain ranges (Table 4). After the islands were isolated by the contraction of boreal habitats to approximately their present position, extinctions reduced the faunas of each island and thus played a major role in determining species composition. Five large islands have retained at least 10 of their original 14 species, but five small islands have lost all but 3 or 4 of the original set of species in the period of approximately 10,000 years that the boreal habitats have been isolated. The distribution of extinctions among species is highly non-random and appears to be related primarily to population size, as MacArthur and Wilson (1967) predicted. Herbivorous species of generalized habitat requirements and small to intermediate body size have persisted on

most of the islands (Table 4). In contrast, herbivores of large body size and/or specialized habitat requirements and carnivores have had higher extinction rates and persist on only a small proportion of the 19 islands. The frequency of occurrence of boreal species on the islands (Table 4) corresponds very closely to the relative abundance of these species where they occur together on large islands or continental mountain ranges (personal observations). The dependence of extinction on population size probably is even more precise than is apparent here, because population size is influenced by the presence of particular habitats and competing species which vary among islands. For example, one of the few mountain ranges where a juniper-pinyon chipmunk (*Eutamias dorsalis* or *E. panamintinus*) does not occur is the Ruby Mountains, where juniper-pinyon woodland is very poorly de-

veloped. Similarly, the chipmunk characteristic of higher elevations (*Eutamias umbrinus*) is absent from the Pilot Range, which has only small stands of mixed conifers on its single tall peak. On this mountain, in the absence of *E. umbrinus*, *E. dorsalis* has extended its altitudinal range upward into the mixed conifers on the peak.

CONCLUSIONS, PREDICTIONS, AND UNANSWERED QUESTIONS

The insular distributions of boreal birds and mammals in the Great Basin differ in ways that are consistent with both current biogeographic theory and independent evidence of ecological and historical factors that have affected colonization and extinction. All data seem consistent with the interpretation that insular bird populations represent an equilibrium between contem-

TABLE 4. Characteristics of the boreal mammal species that inhabit the montane islands of the Great Basin. Species are listed in decreasing order of frequency of occurrence.

Species	Body weight (grams)	Diet	Habitat	Number of islands inhabited
<i>Eutamias umbrinus</i>	60	mostly seeds	generalist: forests, woodlands, talus	17
<i>Neotoma cinerea</i>	300	green vegetation	generalist: rock outcrops or talus in all habitats	17
<i>Eutamias dorsalis</i> , <i>E. panamintinus</i>	55	mostly seeds	generalist: primarily juniper-pinyon woodlands	16
<i>Spermophilus lateralis</i>	170	green vegetation seeds	generalist: open forest, meadow	14
<i>Microtus longicaudus</i>	45	green vegetation	generalist: meadow, open forest, streams	13
<i>Sylvilagus nuttallii</i>	800	green vegetation	generalist: all habitats except dense forest	12
<i>Marmota flaviventris</i>	3,000	green vegetation	generalist: open forest, meadow	10
<i>Sorex vagrans</i> , <i>S. tenellus</i> ¹	7	invertebrates	generalist: forest, meadow, streams	8
<i>Sorex palustris</i>	14	invertebrates	permanent streams	6
<i>Ochotona princeps</i>	120	green vegetation	talus adjacent to meadow	5
<i>Zapus princeps</i>	25	seeds, green vegetation	wet meadow, streams	4
<i>Mustela erminea</i>	50	small vertebrates	generalist: meadow, open forest	4
<i>Spermophilus beldingi</i>	300	green vegetation	wet meadows	3
<i>Lepus townsendii</i>	3,000	green vegetation	large open meadows	1

¹Congeners listed on the same line are ecological and geographic replacements.

porary rates of colonization and extinction; immigration rates are sufficiently high that boreal bird populations inhabit almost all islands where there are suitable habitats, regardless of their isolation from continents. In contrast, the boreal mammal populations represent relicts of species that were widespread in the Great Basin during the late Pleistocene when habitat bridges connected the islands and continents; the mammal faunas of the islands have been derived from a common set of Pleistocene colonists by subsequent extinctions in the absence of immigration.

Neither the avian nor the mammalian distributions fit the equilibrium model proposed by MacArthur and Wilson (1967) to account for diversity on oceanic islands. The insular mammal faunas clearly are not in equilibrium; in the absence of immigration they are gradually relaxing toward an equilibrium of zero species at rates inversely related to island size. The distribution of birds does represent a sort of equilibrium between contemporary colonization and extinction, but the immigration rates are so high that the islands are virtually saturated with species for which the appropriate habitats are present. The avifaunas of the islands differ from the MacArthur-Wilson model in that there is no significant effect of isolation by distance, species composition is quite precisely determined by habitat, and rates of faunal turnover probably are very low (see Brown and Kodric-Brown 1977).

The information available on the distribution of other vertebrates among insular habitats suggests that the kinds of patterns described here for birds and mammals may be widespread. Migratory birds, bats, and very large carnivorous and herbivorous mammals probably are at least as vagile as permanent resident boreal birds. They would be expected to colonize most suitable habitats and show little effect of insular extinction or isolation by distance. On the other hand, amphibians and reptiles probably have dispersal capacities similar to mammals. These

taxa are unlikely to cross habitat barriers of even modest extent, and it is well known that fishes can colonize new areas only when suitable habitat bridges are present (Barbour and Brown 1974, Hubbs and Miller 1948, Hubbs et al. 1974, Smith, this symposium). The distributions of these taxa should be extremely sensitive to paleoclimatic and geological events; where insular habitats have been connected and reisolated they should show relictual distributions in which the identity of the colonists and the effects of subsequent extinctions produce patterns of diversity comparable to those of the small boreal mammals. It is interesting to speculate that the extremes of vagility which characterize most of the vertebrates and the extensive climatic and geological changes that have drastically changed the landscape of western North America within the last million years make it unlikely that land and fresh water vertebrates in this region will show the sort of equilibrium distributions that have been demonstrated for the biotas of oceanic islands with a long history of isolation and relative environmental stability (see MacArthur and Wilson 1967, Simberloff 1974).

In insular biogeography many important questions remain to be answered, and much theoretical and empirical work is yet to be done before this promising and vigorous young science can afford to rest on its laurels. The vertebrates that are distributed among the numerous isolated habitats in western North America continue to offer great potential as systems for testing theory and developing general concepts. For those organisms that appear to demonstrate equilibrium distributions it is particularly important to measure turnover rates accurately, and to incorporate the results into an appropriate conceptual framework. For those organisms that exhibit relictual distributions it is important to elucidate patterns of colonization and extinction and to relate those to theory. Three generations of ichthyologists (Hubbs and Miller 1948, Hubbs et al. 1974, Smith, this symposium) have carefully dis-

sected historical changes in Great Basin drainages and have related them to the contemporary distribution of fishes. As yet there has been little attempt to relate these patterns to biogeographic theory, but the possibilities for doing so seem great and it is hoped it will be attempted soon. The distributions of many organisms are patchy on scales smaller than the gross biogeographic one considered here. Smith (1974a, b) has obtained some encouraging results by using the theory of insular biogeography and the dynamics of opposing colonization and extinction rates to account for the distribution of a small boreal mammal (*Ochotona princeps*) among the isolated patches of its specialized rockslide habitat in the Sierra Nevada. It will be interesting to see to what extent this approach continues to prove useful for understanding insular distributions on various scales.

ACKNOWLEDGMENTS

This paper could not have been written without the field work and published species lists of numerous collectors, systematists, and biogeographers who have worked to document the distributions of birds and mammals in the Great Basin. I am particularly grateful to N. K. Johnson for providing most of the data on birds and to W. H. Behle for making available information presented in this symposium. My wife, A. Kodric-Brown, and my students have done much to encourage my work in insular biogeography. I would like to dedicate this paper to the memory of Stephen D. Durrant, whose knowledge of the Great Basin and its mammals was matched only by his enthusiasm for the outdoor life and his ability as a teacher and storyteller.

APPENDIX 1. Records of occurrence of permanent resident boreal bird species.¹

Species	Sample Area																	
	1	2	3	4	8	9	10	11	14	15	16	18	19	20	21	22	23	
<i>Dendragapus obscurus</i>	x			x	x			x	x	x	x	x	x	x	x		x	
<i>Bonasa umbellus</i>																x	x	
<i>Lagopus leucurus</i>																	x	
<i>Oreortyz picta</i>	x	x		x										x	x			
<i>Glaucidium gnoma</i>			x				x							x	x	x	x	
<i>Strix occidentalis</i>														x	x	x	x	
<i>S. nebulosa</i>															x			
<i>Dryocopus pileatus</i>															x		x	
<i>Dendrocopos villosus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>D. pubescens</i>					x					x	x	x	x			x	x	
<i>D. albolariatus</i>														x	x			
<i>Picoides arcticus</i>														x	x			
<i>P. tridactylus</i>										x						x	x	
<i>Perisoreus canadensis</i>																x	x	
<i>Cyanositta stelleri</i>	x		x			x		x		x	x	x	x	x	x	x	x	
<i>Parus gambeli</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Sitta carolinensis</i>	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x	
<i>S. pygmaea</i>	x					x	x			x				x	x	x	x	
<i>Cinclus mexicanus</i>	x			x	x	x				x	x	x	x	x	x	x	x	
<i>Pinicola enucleator</i>														x	x	x	x	
Total	8	5	4	6	6	6	5	5	4	9	7	6	6	13	15	15	16	

¹Data from Johnson (1975) and Behle (this symposium).

APPENDIX 2. Records of occurrence of small boreal mammal species.¹

Species	Sample Area																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Sorex lyelli</i>																							
<i>S. trochiloides</i>																							
<i>S. vagrans</i>																							
<i>S. tenellus</i>																							
<i>S. palustris</i>																							
<i>Martes americana</i>																							
<i>Mustela erminea</i>																							
<i>Aplodontia rufa</i>																							
<i>Marmota flaviventris</i>																							
<i>Spermophilus armatus</i>																							
<i>S. bellingeri</i>																							
<i>S. lateralis</i>																							
<i>Eutamias alpinus</i>																							
<i>E. townsendii</i>																							
<i>E. dorsalis</i>																							
<i>E. amoenus</i>																							
<i>E. quadrimaculatus</i>																							
<i>E. quadrivittatus</i>																							
<i>E. umbrinus</i> ¹																							
<i>E. panamintinus</i>																							
<i>E. spectiosus</i>																							
<i>Tamiasciurus ludsonicus</i>																							
<i>T. douglasii</i>																							
<i>Glaucomys sabrinus</i>																							
<i>Neotoma ciueca</i>																							
<i>Phacocorys intermedia</i>																							
<i>Clethrionomys gapperi</i>																							
<i>Microtus longicaudus</i>																							
<i>M. richardsoni</i>																							
<i>Zapus princeps</i>																							
<i>Ochotona princeps</i>																							
<i>Lepus townsendii</i>																							
<i>L. americanus</i>																							
<i>Sylvilagus nuttallii</i>																							
Total	11	3	7	13	10	4	4	12	6	3	5	7	8	4	10	8	3	6	22	23	16	21	21

¹Data from Durrant (1952), Durrant et al. (1955), Grinnell (1933), Grinnell and Storer (1924), Hall (1946), Museum of Zoology at the University of Utah, and my own field work. Includes *Sorex obsoletus*. Includes *Eutamias palmeri*.

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BIOGEOGRAPHY AND MANAGEMENT OF NATIVE WESTERN SHRUBS: A CASE STUDY, SECTION TRIDENTATAE OF ARTEMISIA

E. Durant McArthur and A. Perry Plummer¹

ABSTRACT.—Biogeographical considerations are important in the management of western shrublands. Seedings on rangelands have a higher probability of success when tried and tested principles are followed. It is usually best to seed mixtures that include adapted shrubs and herbs. Shrubs generally are well adapted to the environmental extremes of western ranges. Throughout the year, they provide nutrients for herbivores that are only seasonably available in herbs.

Section *Tridentatae* of *Artemisia* is endemic to western North America and distinct from the analogous Eurasian section (or subgenus) *Seriphidium*. The groups have separate, distinguishable centers of diversity; the two groups seem to be connected in the geologic past by way of the more primitive subgenus *Artemisia*. Preliminary karyotypic evidence suggests different but advanced karyotypes for both groups; chemotaxonomic and morphological data indicate differences in the groups. The *Tridentatae* likely evolved in North America during late Tertiary or early Quaternary times under the stimulus of cycles of aridity.

The *Tridentatae* (sagebrushes) are morphologically variable. Different accessions are differentially adapted. Management practices for various taxa should take into consideration the individual taxon's characteristics. Effort should be made to seed adapted taxa and accessions. Sagebrush management requires maintenance, seeding, or thinning, depending upon the circumstances.

Aside from serving as a review of the literature, this paper presents original data and touches upon unpublished material and reports being prepared for publication.

Shrubs are an important component of the vegetation of the American West, as well as in other parts of the world. In fact, much of the West is classified as shrubland because the dominant plant species are shrubs (Küchler 1964, McGinnies 1972). Plummer (1974) recognized six major shrubland types in the American West.

Since the arrival of the white man, shrub ecosystems have been exploited and despoiled by his livestock and land management practices (Cottan 1961, Heady 1975). The distribution and composition of many plant and animal communities have been substantially altered. The relatively new science of range management was born, in part, to systematize efforts to make shrublands more productive. The value of shrubs in their own right has long been under-

estimated (McKell 1975b). In fact, much effort, time, and money have been spent to eradicate and control shrubs in order to facilitate the establishment of exotic grass monocultures.

Shrubs have many current and potential uses. In the proceedings of an international symposium on useful wildland shrubs (McKell et al. 1972), a section on the present and possible uses of shrubs included chapters devoted to browse and cover for wildlife, low-maintenance landscaping, soil cover and stabilization, fire relations, medicinal values, and industrial raw materials. This list was not exhaustive; for example, no reference is made to the use of shrubs as food for livestock.

Our work on shrubs began with a need to improve critical winter game ranges (Plummer et al. 1968) and has continued with emphasis shifting to improving all types of disturbed sites (McArthur et al. 1974, Monsen 1975, Plummer, in press). Numerous

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species and ecotype adaptation plots have been set out both in and out of the natural ranges of particular shrub taxa. Plummer (in press) listed 85 native and 14 exotic shrubs that have proved to be adapted to disturbed sites in one or more vegetative communities of the Intermountain Region. Some shrubs can be established only vegetatively or by transplanting and do not reproduce by seed. Even these, however, have value since they cover and stabilize disturbed areas and serve as a nurse crop on critical sites for plants that establish more slowly.

A principal thrust of range management has been in the modification of vegetation—often disclimax vegetation (Heady 1975). Mechanical, chemical, and burning methods have been used widely to control unwanted plants—mostly woody ones—on rangelands. These treatments are generally followed by seeding. Practical trials and experiments have succeeded and failed often enough for cause and effect relationships to be analyzed and to serve as a set of principles. Recommendations relative to the seeding of many range sites can be made with a high probability of success. Plummer et al. (1968) and Heady (1975) outlined procedures and site criteria necessary for successful range seedings. Except for weather conditions, these are controllable by the range manager. We wish to emphasize, as did Plummer et al. (1968) and Heady (1975), the importance of planting mixtures of adapted taxa because:

- (1) Many seedings are on variable terrain that includes diverse microhabitats.
- (2) A mixed diet is usually more palatable to and nutritious for herbivores.
- (3) Periods of growth vary for different plant taxa and classes (shrubs, forbs and grasses); so succulent forage is provided for a longer time.
- (4) Some plants benefit others by providing habitat and nutrients.
- (5) Diseases and insect pests do not attack all species equally. Shrubs should be included in most seedings since they are well adapted to drought, salinity, acidity, wide temperature fluctuations, and other environmental extremes of western ranges. In addition, they provide habitat for ani-

mals that other classes of plants do not (McKell 1975a).

This paper examines the biogeography and the management implications of a particular group of shrubs—the sagebrushes, section *Tridentatae* of *Artemisia*. The sagebrushes are perhaps the most common shrub in western North America. In order to get a better idea of how to better manage and utilize this resource, we have tried to catch a glimmer of its evolutionary past. Such information should benefit the management of sagebrush ranges by providing bases for better understanding species adaptation and distribution and plant improvement programs through hybridization and selection.

METHODS AND MATERIALS

Species Distributions.— General distribution of species of the *Tridentatae* was obtained from Ward (1953), Beetle (1960), and by examining the *Artemisia* collections of the herbaria of Brigham Young University (BRY) and the Intermountain Station's Shrub Sciences Laboratory (SSLP). We have followed Beetle's (1960) and Beetle and Young's (1965) nomenclature for the *Tridentatae* (Fig. 1). Distribution of the *Seriphidium* species that occurs in the Soviet Union was taken from Polyakov (1961). For species that occur outside the Soviet Union, de Candolle (1838) and Boissier (1875) were consulted (Fig. 2). We reviewed other regional and national floras peripheral to the Soviet Union but found little information to add to the aforementioned references.

Karyotyping.— The karyotypes of section *Tridentatae* were obtained from a preliminary analysis of data for a later report (McArthur, Pope, and Plummer, in preparation). A sample cell was selected from each of 13 diploid and 14 tetraploid populations representing 9 diploid and 9 tetraploid taxa. Squashed root tips of seedlings were microscopically analyzed. The slides were prepared by fixing colchicine-pretreated root tips in 1:3 acetic alcohol and squashing them in acetocarmine. The idiogram of section *Tridentatae* (Fig. 3) was prepared from measurements made on 20 X 25 cm photomicrographic prints at a magnification of 3120X. The idiogram for the two species of

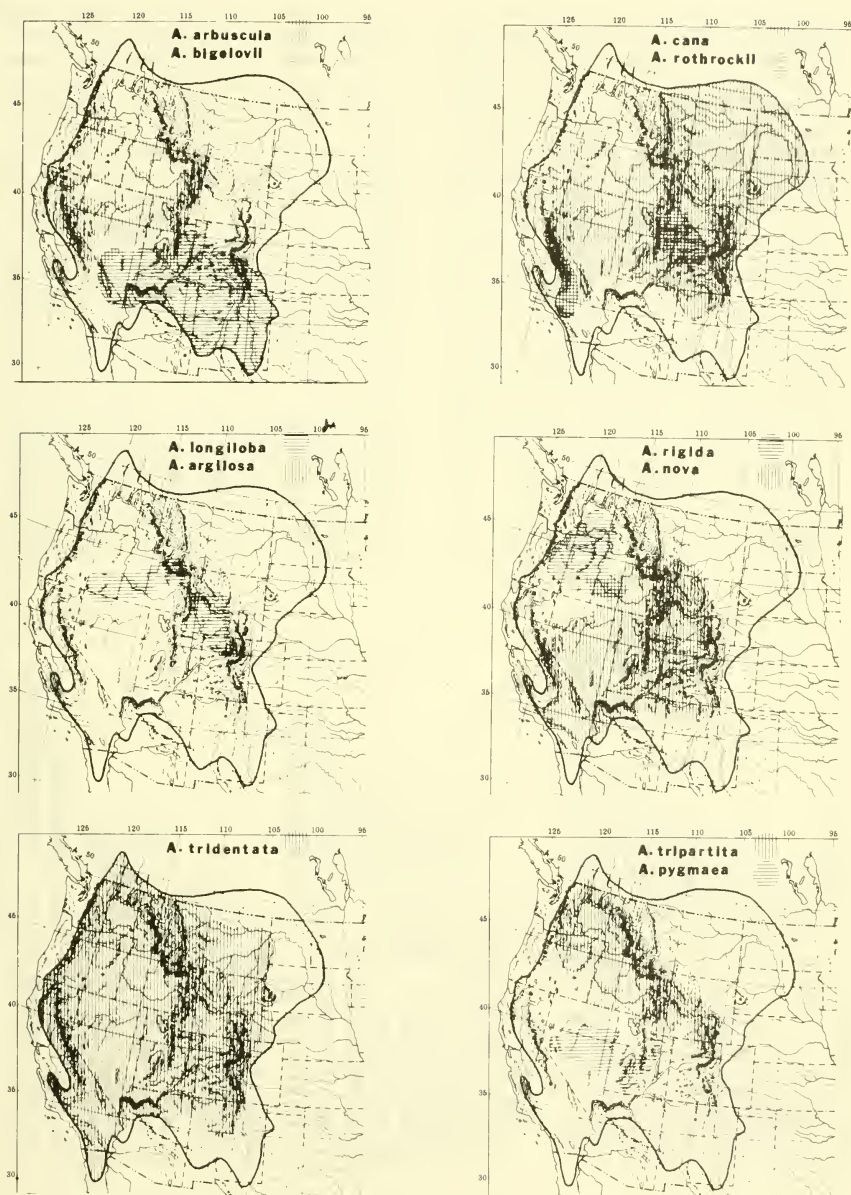


Fig. 1. Distribution ranges of the species of section *Tridentatae*.

Seriphidium (Fig. 3) was prepared from data presented by Filatova (1974). We used the shorter of two lengths Filatova gives for chromosome 3 of *A. juncea*. Chromosome sizes (L = large, M = medium, S = small) were determined by pairing the chromosomes according to relative length and centromere position, dividing the genome into relative lengths, averaging the length of each pair, and proportionalizing the pair so the genome had a length of 100 arbitrary units. Thus, $L > 12.4$, $M = 9.6 - 12.4$, $S < 9.6$ for diploids and $L > 6.2$, $M = 4.8 - 6.2$, $S < 4.8$ for tetraploids. The centromere positions (M = metacentric, SM = submetacentric, and ST = subterminal) were determined by the ratio of the length of the short arm to the length of the long arm. Thus, $M > 75$ percent, $SM = 50 - 75$ percent, $ST < 50$ percent (Tables 1 and 2).

Species Adaptation.— Shrub wildings have

been collected in the spring (March-June) and fall (October-November) and transplanted to uniform gardens and smaller species adaptation plots. Periodic ratings are made as to their height, crown, vigor, herbage yield, reproduction, and survival. These data are on file principally at the Great Basin Experimental Area in Ephraim, Utah, but also at the Shrub Sciences Laboratory in Provo, Utah. Collection numbers, prefixed by a U, have been assigned to accessions within each taxon (Tables 1, 2, 3). Voucher herbarium specimens are deposited at the Shrub Sciences Laboratory (SSLP).

SECTION TRIDENTATAE OF ARTEMISIA

The genus *Artemisia* is a group of about 200 plant species which belong to the tribe Anthemideae of Compositae (de Candolle 1837, Clapham 1962). Good (1974) considers *Artemisia* as belonging to his temperate genera, group 1, subgroup 2, which includes

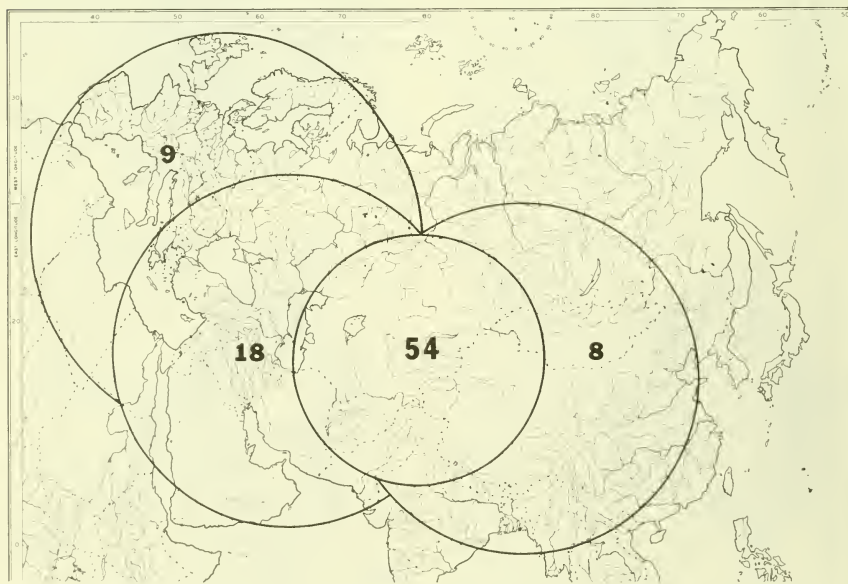


Fig. 2. Distribution of the section (subgenus) *Seriphidium* in Eurasia and North Africa. The numbers indicate maximum number of species in each area.

"genera found throughout the northern extratropical latitudes with some extension southwards in all directions, usually to certain tropical mountains only."

Besser (1829) began the first comprehensive monograph on the genus early in the 19th century. He recognized four sections—Abrotanum, Absinthium, Dracunculus, and Seriphidium. His monograph was not completed before he died, but de Candolle's (1837) "Prodomus Systematis Naturalis" and Hooker's (1840) "Flora Boreali-Americana" include significant portions of Besser's work. Besser's sections are still considered the principal divisions of the genus, but in some treatments they have been elevated to the rank of subgenus and additional subordinate sections created (Rydberg 1916, Polyakov 1961). The comprehensive treatment of *Artemisia* in the "Flora of the USSR" (Polyakov 1961) unites Absinthium and Abrotanum into the single large subgenus *Artemisia*. Hall and Clements (1923) recognized the close affinity of these two groups, which were separated in Besser's scheme

only by the hairiness of the floral receptacle. Members of *Seriphidium* are distinguished by having only perfect disk flowers whereas members of the other subgenera have fertile or sterile ray flowers and various degrees of disk flower fertility. Rydberg (1916), while recognizing the subgenus *Seriphidium*, created the section *Tridentatae* for most North American members of *Seriphidium*. He also created monotypic sections for *A. rigida* and *A. pygmaea* as well as a new genus for the largely herbaceous *A. palmeri*. More recent monographers (Hall and Clements 1923, Ward 1953, and Beetle 1960) have been more conservative than Rydberg, but have been divided on the retention of *Tridentatae* as a section. Beetle (1960) included all woody, North American, homogamous *Artemisia* species in the section *Tridentatae* along with *A. bigelovii*, which often has a ray flower or two on otherwise discoid heads. Beetle's *Tridentatae* form a group of 11 unequal species endemic to western North America (Fig. 1). The species distribution ranges vary in size from

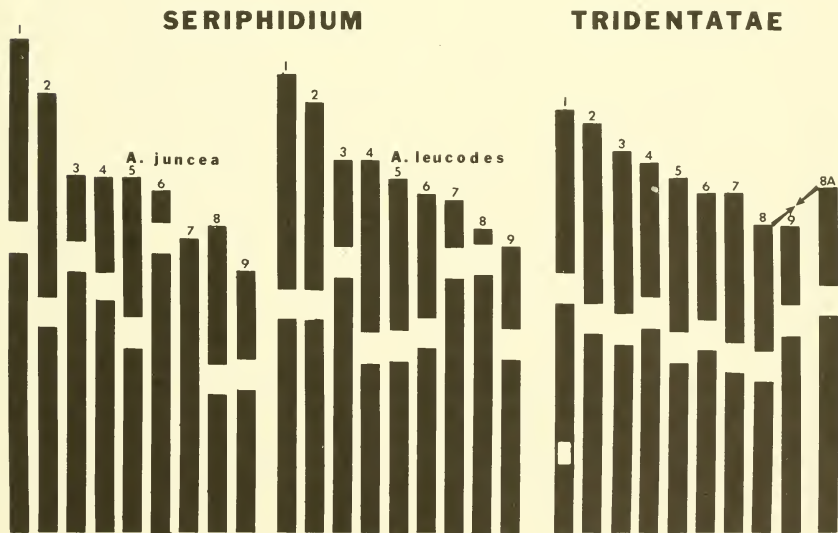


Fig. 3. Idiograms of two species of section *Seriphidium*, *A. juncea*, and *A. leucodes* (after Filatova 1974) and a generalized idiogram of section *Tridentatae*. Note secondary constriction in long arm of the first chromosome in the *Tridentatae*. The arrows indicate a chromosome substitution in some taxa (Table 1).

TABLE 1. Chromosome constitution of representative diploid *Tridentulae*.

Taxon	Collection data	Chromosome															
		1	2	3	4	5	6	7	8	8A	9	trl	trl	trl	trl	trl	trl
<i>Artemisia</i>		trl ^a	trl ^b	trl	trl	trl	trl	trl	trl	trl	trl	trl	trl	trl	trl	trl	trl
<i>arbuscula</i>	U1-Paradise Valley, Humboldt Co., Nevada	12.5	7.2	12.5	6.5	11.8	6.3	11.6	6.7	10.6	5.8	10.6	6.2	10.8	5.6	10.6	7.2
<i>A. arbuscula</i>	U4-Wildsoe, Garfield Co., Utah	11.9	7.1	11.9	6.2	11.7	6.2	11.9	7.1	11.4	5.9	11.0	6.9	10.0	5.3	11.0	7.9
<i>A. bigelovii</i>	U9-Flagstaff, Coconino Co., Arizona	13.8	8.4	13.0	6.7	12.1	6.3	11.7	6.7	11.7	6.3	10.7	6.1	11.7	5.9	10.7	7.5
<i>A. cana</i>	U10-Nolan Station, Carbon Co., Utah	13.2	7.3	13.0	6.5	12.1	6.4	11.7	4.0	10.3	5.2	9.5	5.6	10.3	5.7	9.3	4.7
<i>A. nora</i>	U13-Huntington, Emery Co., Utah	13.0	8.0	13.0	7.3	11.9	6.5	11.6	8.2	11.1	5.7	10.8	6.0	10.8	5.7	8.7	5.4
<i>A. rigida</i>	U34-LaGrande, Union Co., Oregon	13.8	8.1	12.6	6.7	11.4	6.3	11.8	6.9	9.8	4.9	10.3	6.1	10.2	5.6	10.1	6.8
<i>A. rotrockii</i>	U1-Swasey Ridge, Sanpete Co., Utah	14.3	8.1	13.0	6.7	11.3	6.7	12.1	7.4	10.0	5.4	10.8	6.5	9.7	5.0	10.0	5.3
<i>A. tridentata</i>	U44-Loa, Wayne Co., Utah	12.6	7.6	12.6	6.9	11.8	6.3	10.1	6.6	11.1	6.0	9.8	6.5	9.8	5.1	8.8	5.2
<i>A. tridentata</i>	U63-Franklin, Franklin Co., Idaho	14.2	8.4	12.5	6.4	12.2	6.3	11.7	7.1	11.7	6.1	9.6	5.8	10.2	5.3	8.6	4.8
<i>A. tridentata</i>	U9-Bennmore, Tooele Co., Utah	12.6	7.1	13.2	7.0	13.0	7.3	11.6	6.6	11.2	6.0	11.6	7.2	10.0	5.2	9.3	5.2
<i>A. tridentata</i>	U28-Dowd Springs, Daggett Co., Utah	13.3	7.7	12.7	7.1	11.4	6.1	10.5	6.3	11.0	5.7	10.5	6.3	10.1	5.4	10.1	5.8
<i>A. tridentata</i>	U36-Boise, Ada Co., Idaho	13.6	7.4	13.4	6.8	11.8	6.5	10.5	6.5	11.0	5.8	10.0	5.8	10.5	5.5	9.4	5.2
<i>A. tripartita</i>	U2-Dubois, Clark Co., Idaho	12.4	7.4	12.5	6.8	11.6	6.1	11.6	6.8	10.9	5.7	9.7	6.3	10.9	5.5	9.1	4.6
\bar{x}		13.2	7.7	12.8	6.7	11.8	6.4	11.4	6.9	10.9	5.7	10.4	6.2	10.4	5.4	9.3	5.1
se		.2	.1	.1	.1	.1	.1	.2	.1	.2	.1	.2	.1	.2	.1	.2	.2
Type ^d		LSM	LM	MM	MSM	MM	MSM	MM	MSM	MM	MSM	MM	MSM	MM	MSM	SM	SST

^atrl = total relative length of chromosome^btrl = relative length of long arm of chromosome^cChromosome types; the first letter stands for chromosome size, L = large, M = medium, S = small. The other letters stand for centromere position, M = metacentric, SM = submetacentric, ST = subterminal. Some of the LSM have an obvious secondary constriction (Fig. 3); others do not.

those that cover most of the range of section *Tridentatae* (*A. tridentata* and *A. cana*) to relatively small ranges covering about 10 percent of the section's range (*A. pygmaea* and *A. longiloba*) to the restricted type location range of *A. argilosa*. *A. rothrockii* is shown with a disjunct range (Fig. 1). Ward (1953) and Cronquist (1974) maintain that *A. rothrockii* is restricted to the Sierra Nevada and its outliers. Beetle (1960), on the other hand, records the species from the Rocky Mountains. The California material is tetraploid and hexaploid (Ward 1953), whereas our work indicates that Rocky

Mountain material (from Utah's Wasatch Plateau) is diploid (McArthur, Pope, and Plummer, in preparation). The Rocky Mountain material may be an undescribed taxon. However, in this paper, we are treating it as *A. rothrockii*.

EVIDENCE FOR SEPARATING TRIDENTATAE FROM SERIPHIDIUM

Regardless of the rank (subgenus or section) that one attaches to *Tridentatae* or *Seriphidium*, the two taxa should be separated. Hall and Clements (1923), Ward

TABLE 2. Chromosome constitution of representative tetraploid *Tridentatae*.

Taxon	Collection data	Chromosome pair types ^a							
		LSM	LM	MM	MSM	MST	SM	SSM	SST
<i>Artemisia arbuscula</i>	U3-Antimony, Garfield Co., Utah	3	4	2	3	1	1	2	2
<i>A. bigelovii</i>	U9-Flagstaff, Coconino Co., Arizona	2	2	5	3	1	2	1	2
<i>A. bigelovii</i>	U13-Chinle, Apache Co., Arizona	3	2	5	3	1	2		2
<i>A. cana</i>	U3-Strawberry Reservoir, Wasatch Co., Utah	2	4	4	2	1	1	2	2
<i>A. nova</i>	U16-John's Valley, Garfield Co., Utah	3	1	6	2	1		3	2
<i>A. nova</i>	U22-Steinaker Reservoir, Uintah Co., Utah	3	1	5	3	2	2	1	1
<i>A. pygmaea</i>	U1-John's Valley, Garfield Co., Utah	2	2	6	4	1		1	2
<i>A. rigida</i>	U5-Elder Flat, Monow Co., Oregon	2	1	8	3	2			2
<i>A. tridentata tridentata</i>	U75-Wingate Mesa, San Juan Co., Utah	2	4	4	2		2	2	2
<i>A. tridentata tridentata</i>	U89-Steptoe Valley, White Pine Co., Nevada	2	4	4	2		2	2	2
<i>A. tridentata vaseyana</i>	U14-Colton, Utah Co., Utah	2	2	6	3		2	1	2
<i>A. tridentata vaseyana</i>	U23-Pinto Canyon, Washington Co., Utah	2	2	6	3	2		1	2
<i>A. tridentata wyomingensis</i>	U61-Milford, Beaver Co., Utah	2	2	8	3		1	1	1
<i>A. tridentata wyomingensis</i>	U80-Jacob's Lake, Coconino Co., Arizona	2	3	6	3		2		2
Average		2.3	2.4	5.4	2.8	.9	1.2	1.2	1.8
Expected		2.0	2.0	6.0	4.0	0	2.0	0	2.0

^aChromosome types: The first letter stands for chromosome size; L = large, M = medium, S = small. The other letters stand for centromere position; M = metacentric, SM = submetacentric, ST = subterminal. Some of the LSM have an obvious secondary constriction, others do not.

TABLE 3. Establishment and survival of *Artemisia tridentata* wilding transplants at the Snow Field Station, Ephraim, Utah.

Subspecies	Collection data	Number of plants			Percent 1976/1971	Vigor ^a	Repro- duction ^b
		Initial (1969-1970)	Established (1971)	Survivors (1976)			
<i>Tridentata</i>	U44-Loa, Wayne Co., Utah	33	17	11	64.7	4	7
	U74-Dove Creek, Dolores Co., Colorado	40	31	25	80.6	9	10
	U75-Wingate Mesa, San Juan Co., Utah	47	36	22	61.1	7	4
	U76-Clear Creek Canyon, Sevier Co., Utah	44	33	21	63.6	6	5
	U79-Dog Valley, Juab Co., Utah	46	46	44	95.7	10	10
	U82-Brush Creek, Uintah Co., Utah	25	21	14	66.7	7	7
Total		235	184	137			
Mean					74.4	6.1	7.2
<i>Vaseyana</i>	U13-Indian Peaks Beaver Co., Utah	41	41	24	58.6	6	7
	U14-Colton, Utah Co., Utah	74	65	45	69.2	8	3
	U15-Sardine Canyon, Cache Co., Utah	41	24	20	83.3	5	7
	U19-Salina Canyon, Sevier Co., Utah	17	9	7	77.8	3	4
	U23-Pinto Canyon, Washington Co., Utah	36	28	26	92.9	7	7
	U24-Clear Creek Canyon, Sevier Co., Utah	44	34	12	35.3	4	3
	U31-Durkee Springs, Sevier Co., Utah	32	28	14	50.0	7	2
	U52-Alton, Kane Co., Utah	16	7	3	42.9	3	6
	U72-Petty Bishop's Log, Sanpete Co., Utah	124	99	88	88.9	8	8
Total		425	335	239			
Mean					71.3	5.7	5.2
<i>Wyomin- gensis</i>	U17-Milford, Beaver Co., Utah	41	15	10	66.7	7	4
	U37-Evanston, 23 Uinta Co., Wyoming	23	8	4	50.0	8	2
	U58-Trough Springs, Humboldt Co., Nevada	63	26	14	53.8	5	3
	U80-Jacob's Lake, Coconino Co., Arizona	42	22	17	77.3	8	4
Total		169	71	45			
Mean					63.4	7.0	3.2

^aVigor rating is an ocular estimate of the accession's general condition 1 = all dead; 5 = average vigor with some dieback; 10 = exceptional vigor with little or no dieback.
^bReproduction rating is an ocular estimate of the accessions reproduction: 1 = none; 5 = seedlings common but even aged; 10 = seedlings abundant and of several age classes.

(1953), and Beetle (1960) all recognized the distinctness of the North American forms, although each treated them in a different manner. We believe there are several compelling reasons for separation, which we will discuss.

Members of *Seriphidium* are Eurasian (and North African). Their center of distribution is Central Asia (Fig. 2). The present distribution suggests an evolutionary radiation from the areas of greatest species diversity. On the basis of karyotypic, anatomical, and morphological evidence, Filatova (1974) supported the view that the most primitive members of the *Seriphidium* occur in arid areas in Kazakhstan, USSR and adjacent areas in Central Asia. She suggested an annual/biennial herbaceous species (*A. leucodes*) and a perennial shrub (*A. junceus*) as being ancient primitive types. Musaev (1965) gave detailed distribution maps of five species of *Seriphidium*, which indicate that the northern limit for these species is about 52°-53° N. latitude. Musaev contended that the Turan flora, composed in part of these *Seriphidium* members, is southern and Mediterranean and not strongly connected to the northern (grass-forb) steppes. This body of evidence suggests that Eurasian *Seriphidium* originated in Central Asia and radiated outward. Few members of the *Seriphidium* are found in northerly latitudes. The most widespread northern Old World species, *A. martima* (*sensu lato*) (Polyakov 1961, Clapham 1962), may have been able to migrate north in milder coastal habitats. The North American *Tridentatae* and at least two other *Artemisia* species remain problematical—*A. palmeri* and *A. mendozana*. *Artemisia palmeri* is largely herbaceous, is endemic to coastal badlands on both sides of the California-Baja California border, and little resembles the *Tridentatae*. Rydberg (1916) created a new genus for it—*Artemisiastrum*. *Artemisia mendozana*, presumably from west central Argentina, is little known, but *Artemisia*, in general, is not prominent in South America (Bonpland et al. 1820, Harvard Univ. 1968, Heusser 1971, Good 1974). It was listed as a member of the *Seriphidium* by de Candolle (1837); Kawatani and Ohno (1964) indicated

that it was an octoploid ($2n = 72$).

Then, the fact that the *Seriphidium* and *Tridentatae* are advanced taxa, occurring in widely disjunct areas with no discovered pollen record in *Artemisia* profiles of the Beringia (Northeast Siberia-Alaska) area, further supports their taxonomic separation. *Artemisia* is a phylogenetically advanced genus in an advanced family (Compositae) (Stebbins 1974). Present consensus (Carlquist 1966, Cronquist 1968, Stebbins 1974) supports a woody ancestral prototype for the Compositae. However, woodiness in *Artemisia* is probably secondary. Most woody *Artemisia* species are bunched in *Seriphidium* and *Tridentatae*, which are specialized (reduced) in floral characteristics (Hall and Clements 1923). Anatomical characteristics of *Tridentatae* stems suggest an herbaceous ancestry (Diettert 1938, Moss 1940, Stebbins 1974). The *Seriphidium* do not presently occur in northeastern Siberia nor the *Tridentatae* occur in Alaska or adjacent areas of Canada (Fig. 1, 2). On the other hand, members of both the subgenera, *Dracunculus* and particularly *Artemisia* (*sensu lato*), grow in those areas and span, or nearly span, Beringia (Rydberg 1916, Mizushima 1972, Korobkov 1972, Yurtsev 1972). No palynological evidence has been found to indicate that *Seriphidium* or *Tridentatae* were ever in Beringia (Hopkins 1967, Graham 1972). Most pollen identification of Beringian *Artemisia* is only to the genus level; those samples that are identified to species are from the subgenus *Artemisia*. Furthermore, paleobotanists infer from present distributions and climates that *Artemisia* pollen from Quaternary deposits came from herbaceous species of the subgenus *Artemisia* (Colinvaux 1967, Johnson and Packer 1967, Kind 1967). Although *Artemisia* is fairly common in Beringia, it is apparently not as prevalent as it was earlier during Quaternary time and reflects a harsher present day climate (Colinvaux 1967). Woody *Chenopodiaceae* of the same genera, but different species, often grow in association with the *Tridentatae* in North America and the *Seriphidium* in Central Asia (Musaev 1965, Blauer et al. 1976). Stebbins (1974)

believes that both chenopod shrubs and *Artemisia* shrubs of the Tridentatae and Seriphidium evolved from herbaceous ancestors on xeric "islands" of the Arcto-Tertiary Forest. In the case of *Artemisia*, the principally herbaceous, florally primitive subgenus *Artemisia* probably served as parental stock.

The limited data so far available indicate that the basic karyotypes of Tridentatae and Seriphidium are significantly different. Filatova (1974) presented idiograms of two species of Seriphidium which she considered to be primitive (Fig. 3), but Polyakov (1961) listed these taxa as being advanced. Currently, those two idiograms are the only ones available for diploid Seriphidium. We are preparing and will publish karyotypes of several Tridentatae taxa (McArthur, Pope, and Plummer, in preparation). Information presented here is tentative, coming as it does from small samples. Although there is variation throughout the section (Table 1), it appears that one basic genome is present which (with small changes) accounts for the chromosomal variation in the Tridentatae. Further evidence for one basic genome in the Tridentatae is the high incidence of multivalent formations in polyploid populations (McArthur and Pope 1975, McArthur, Pope, and Plummer, in preparation). Generally, diploid Tridentatae have a pair of large submetacentric chromosomes which may have a secondary constriction in the long arm (Fig. 3), a pair of large metacentric chromosomes, three pair of medium metacentric chromosomes, two pair of medium submetacentric chromosomes, a pair of small metacentric chromosomes, and a pair of small subterminal chromosomes. In some cases (Table 1) a pair of medium subterminal chromosomes replaces the small metacentric chromosomes. The karyotype of tetraploid Tridentatae would appear to be an approximate doubling of the diploid karyotype (Table 2).

Karyotype evolution in several Compositae taxa often leads to: (1) shortening of absolute chromosome length, (2) less homogeneity in chromosome lengths within the complement, and (3) rearrangements of chromosomal materials resulting in terminal centromere positions (Stebbins 1953, Huzi-

wara 1962, DeJong 1965, Anderson 1966, 1970). Based on these criteria, both the Seriphidium and Tridentatae have advanced karyotypes as their morphologies suggest. Unpublished data (McArthur, Shrub Sciences Laboratory) indicate some American members of the subgenera *Dracunculus* and *Artemisia* have simpler karyotypes.

Chemotaxonomic studies have shown that section Tridentatae is a more or less natural group (Hanks et al. 1973, Kelsey et al. 1973, Geissman and Irwin 1974). Seriphidium members are probably less homogeneous owing to their greater numbers and wider distribution. However, a particular sesquiterpene lactone, the anthelminic santonin, occurs widely in the old world Seriphidium (Polyakov 1961), but santonin has not been discovered in any of the Tridentatae (Geissman and Irwin 1974).

The Tridentatae are all woody shrubs, whereas about 15 percent of the Seriphidium are herbaceous and others are semi-shrubs with woody bases and herbaceous tops (Hall and Clements 1923, Polyakov 1961).

ORIGIN OF THE TRIDENTATAE

Artemisia is much more richly developed in Eurasia than it is in the Western Hemisphere. Consensus places the origin of the genus in Eurasia (Hall and Clements 1923, Beetle 1960, Stebbins 1974). Some workers, for example, Beetle (1960), believe that the section Tridentatae migrated to North America in a differentiated form. We believe, however, that the North American Tridentatae differentiated in situ from herbaceous ancestors in the subgenus *Artemisia*. This subgenus is circumpolar at present, and evidence indicates that it was formerly even more prevalent in the northern latitudes (Colinvaux 1967, Estes 1968). Hall and Clements (1923) pointed out that *A. bigelovii* shared traits found both in *Abrotanum* (*Artemisia*) and Seriphidium (Tridentatae). They thought *A. bigelovii* or *A. bigelovii*-like stock gave rise to the Tridentatae in the Southwest during the Pleistocene. They believed that with subsequent warming and drying, Tridentatae ancestors migrated north and developed into present-day taxa.

A study on the distribution of chromatographic patterns of phenolic constituents by Hanks et al. (1973) supports this view.

In either case, the *Tridentatae* have only been a prominent part of western American flora since the late Tertiary or early Quaternary periods (Axelrod 1950). The first *Artemisia* pollen recorded in the Intermountain Region is from Miocene Epoch deposits (Tidwell et al. 1972). *Tridentatae* progenitors probably were present on xeric "islands" in or near the North American Tertiary floras (Axelrod 1950). Alternating moist and dry climates during the Pleistocene Epoch favored the repeated evolutionary cycles that provided our present-day *Tridentatae*. Aridity is a powerful evolutionary stimulus (Axelrod 1972, Stebbins 1974).

It is interesting that arid, interior continental climates may have produced independently in western North America and Central Asia analogous series of woody *Artemisia*—the *Seriphidium* and the *Tridentatae*. An apparent similar example of convergent evolution is found in woody chenopod shrubs in the same two areas and in Australia.

MANAGEMENT IMPLICATIONS IN SECTION TRIDENTATAE

Although *Tridentatae* are recognized as a natural group, gross differences among section members have long been recognized. Black sagebrush (*A. nova*) has been regarded as a desirable, palatable species, but big sagebrush (*A. tridentata*) has been considered to be an unwanted range weed (Cottam 1961). We now know there is much variation within these taxa and that palatable and unpalatable forms occur in both (Stevens and McArthur 1974). In addition to the gross differences mentioned, there are many differences of smaller orders of magnitude. These last have led to differences of opinion among taxonomists.

Excluding *A. palmeri*, Rydberg (1916) recognized 13 species of *Tridentatae*, Hall and Clements (1923) 4 species, Ward (1953) 7, and Beetle (1960) 11. Each monographer (except Rydberg) also recognized subspecific taxa. Beetle (1960) and Beetle and Young (1965) divided the *Tridentatae* into 11 spe-

cies, 9 subspecies, and 2 forms. Winward (1970) has suggested an additional form. Although we have learned much about sagebrush in the past 60 years, we have much to learn. Its ubiquitous western presence, its value as a soil stabilizer, its habitat and landscape value, and its attraction to the public will demand attention for a long time.

Range managers will benefit by learning as much as they can about variation in sagebrush. Characteristics of the subspecies of big sagebrush listed in Table 4 illustrate some differences in a group of closely related plants. It is difficult to separate these taxa by any one character, but taken in combination, each taxon is clearly distinct.

Such differences as adaptation, palatability, and height in these as well as in other sagebrush taxa should be taken into account in management decisions. This is not to say a manager should not make decisions on the basis of readily available information. We think that he should, but he should also realize that the knowledge base is expanding.

Some broad aspects of shrub management were discussed in the introduction. We pointed out that some taxa are widely adaptive. In looking at shrub adaptation in a narrower sense, it can be important for us to consider sources of particular taxa individually. On specific sites, different accessions of the same plant taxon may perform differently as do the subspecies of big sagebrush (*A. tridentata*) in a uniform garden (Table 3). Marchand et al. (1966) also observed differential performance of big sagebrush taxa in a uniform garden. As one might expect, the same accessions may perform differently on different sites. Some seem to have broader amplitudes of adaptation than others. In a paired performance (establishment, production, and reproduction) several accessions of *Tridentatae* in the taxa, *A. tridentata tridentata*, *A. nova*, *A. cana*, and *A. bigelovii*, showed differential adaptation. Nine accessions performed equally well at two sites in central Utah (Snow Field Station near Ephraim and Gordon Creek Winter Game Range near Helper), but seven performed markedly better at one or the other of the sites. When considering seed sources for a seeding, it is best to

TABLE 4. Characteristics of subspecies of *Artemisia tridentata*.

Characteristic	Subspecies			References
	<i>tridentata</i>	<i>vaseyana</i>	<i>wyomingensis</i>	
Habitat and range	Foothills and valley floors. 610-2140 m. British Columbia and Montana to Baja California and New Mexico.	Foothills and mountains. 915-3030 m. British Columbia and Alberta to California and New Mexico.	Foothills and valley floors. 1520-2150 m. Montana to Arizona.	This paper; Beetle and Young 1965; McArthur et al. 1974.
Smell	Bitter pungent	Pleasant	Bitter pungent	McArthur et al. 1974.
Leaf shape	Narrowly cuneate to oblanceolate	Cuneate	Cuneate	Marchand et al. 1966; McArthur et al. 1974; McDonough et al. 1975.
Height	1.0-4.0 m	0.7-1.2 m	0.5-0.8 m	McArthur et al. 1974.
Sesquiterpene lactone compounds	4-7	3-6	2	Kelsey et al. 1973.
Ultraviolet visible coumarins	Trace	Abundant	Trace	Shafizadeh and Melinkoff 1970; Stevens and McArthur 1974; Brown et al. 1975.
Tendency to layer	None	Strong	None	Beetle and Young 1965.
Palatability to deer and sheep	Low	High	Intermediate	Hanks et al. 1973; Sheehy and Winward 1976.
Protein content	High	Low	Low	Sheehy and Winward 1976; Welch et al. 1977.
Seed germination	High	Low	Intermediate	Harniss and McDonough 1976.
2n	18,36	18,36	36	Ward 1953; Taylor et al. 1964; Winward 1970; Kelsey et al. 1975;
Flower and seed phenology	Late	Early	Late-Intermediate	McArthur, Pope, and Plummer (in prep.) Marchand et al. 1966; Winward 1970; Hanks et al. 1973.

obtain seed from a site as similar and as close as possible to the site to be seeded. If seed must be brought in from some distance, it is best to get it from a harsher climate or more northerly location (Plummer et al. 1968, Plummer 1977). For example, accessions of *A. bigelovii* from nearby Emery County, Utah, perform much better at the Snow Field Station and the Gordon Creek Winter Range than those from the more distant and southern San Juan County, Utah, and Coconino County, Arizona. Van Epps (1975) presented data supporting a similar conclusion for fourwing saltbush (*Atriplex canescens*). Although the foregoing discussion is based on wilding transplant experiments, we have noted differential success of accessions of big sagebrush on seeded areas.

The sagebrushes are a valuable resource, which can be more valuable if managed wisely. Wise management entails maintaining productive natural populations, seeding to improve depleted or disturbed ranges, and thinning closed stands. When mixed with grasses, forbs, and other shrubs sagebrush adds beauty to the range, food and cover for animals, and stability to the soil. Moreover, sagebrush variation should permit selection of material for particular purposes, such as palatable, high-protein forms for mule deer winter ranges. We think that such an opportunity exists, since putative natural hybrids have been discovered (Ward 1953, Beetle 1960), and we have cytological and artificial pollination data that hybridization occurs (McArthur and Pope 1975, McArthur, Pope, and Plummer, in preparation). We predict that in the years ahead the much-maligned sagebrush will be regarded with increasing favor by land managers.

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NOTE ADDED IN PROOF

Since this paper went to press, we learned of a monographic study on the cytotaxonomy of the *Artemisia maritima* complex of section Seriphidium (Persson, K. 1974. Biosystematic studies in the *Artemisia maritima* complex in Europe. Opera Botanica 35:1-188). Persson's karyotypes of diploid *A. santonicum* are apparently more primitive than those shown by Filatova (1974). However, the *A. santonicum* karyotypes are unlike the *Tridentatae* karyotype.

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APPLYING BIOGEOGRAPHIC PRINCIPLES TO RESOURCE MANAGEMENT: A CASE STUDY EVALUATING HOLDRIDGE'S LIFE ZONE MODEL

James A. MacMahon¹ and Thomas F. Wieboldt^{1,2}

ABSTRACT.—Conservation schemes require some portioning of the world into a discrete number of subunits which might benefit from similar management practices. The Holdridge Life Zone scheme, proposed for such purposes previously, is applied to Utah as an initial test of its usefulness. A hypothetical life zone map was developed entirely on the basis of weather station data and data derived from these values. This predictive map compared favorably to data on patterns of vegetation, mammal, reptile, and amphibian distribution in Utah.

Since the publication of MacArthur and Wilson's (1967) analytical approach to the biogeography of islands, several authors have attempted to apply island biogeography theory to the problem of optimum size and number of nature reserves.

Several aspects of theory have been invoked including species/island area relations (Diamond 1975, Sullivan and Shaffer 1975, Wilson and Willis 1975) and extinction rates (Terborgh 1974). Not all workers agree that this approach is correct or robust (Simberloff and Abele 1976). [See also rebuttals to Simberloff and Abele, e.g., Diamond (1976)]. Simultaneously the theories of island biogeography are being changed or restated in verifiable formats (Simberloff 1976).

Currently economics (Myers 1976) and even international cooperation (Franklin 1977) are being included as factors in nature reserve establishment. Despite all of the interest in the application of theory to practical problems there are few attempts to provide a reasonable plan to test the efficacy and appropriateness of the implied theory/practice merger.

Recently, without judging whether or not theory was adequate or correct, MacMahon

(1977a) suggested a series of concrete steps one might opt to test the various hypotheses. It was hoped that this would be applicable on a world scale.

In summary the suggestion was to determine the most sensitive species to be preserved (i.e., rarest, largest, highest trophic level, most vagile, etc.). This species determines the minimum size of the reserve area. One might also, for a community, use the species area relationship (MacArthur and Wilson 1967). That relationship is

$$S = CA^z$$

where S = number of species, A = island area, C = parameter characteristic of a particular taxon and archipelago and z = power derived by assuming species abundances are distributed in a log normal manner (Preston 1962). The value of C is a community coefficient and not known for most communities. One must also invoke consideration of extinction rates for determining the number of replicate areas necessary (Terborgh 1974).

MacMahon pointed out that if the total world variety of communities was reduced into some small grouping to determine functions like C and determine whether or not there is similar value of C for most ex-

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²Wieboldt reduced some data for this paper. He did not prepare the manuscript and should not be held accountable for the content.

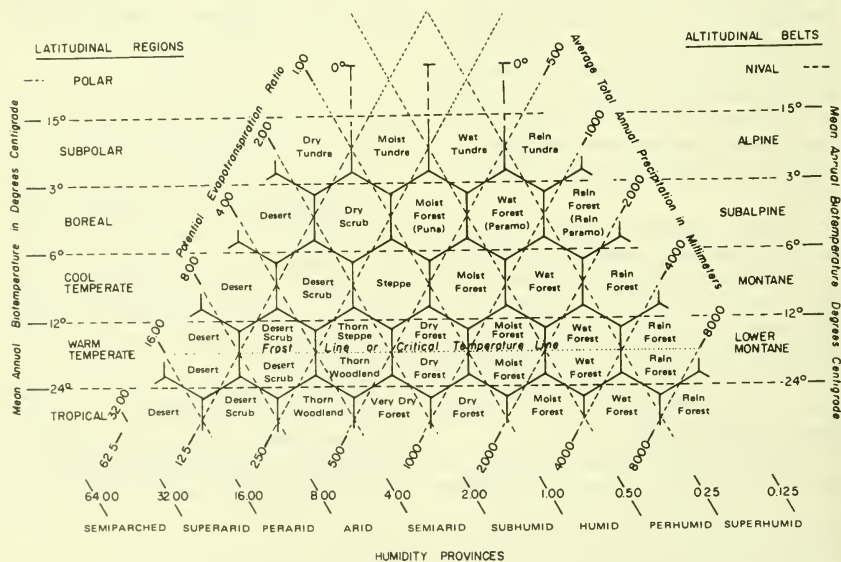
amples of communities within one of these groups, then the conservation process could proceed more rapidly and be applied more broadly.

The suggestion was made that a possible system of classification, often used but seldom tested, was that of Holdridge (1947, 1967). Holdridge's scheme uses mean annual biotemperature (the sum of mean monthly temperature above 0 C divided by 12), mean annual precipitation and potential evapotranspiration to place localities on a chart divided into hexagons representing vegetation types (Fig. 1). Corrections are made for altitudinal differences at similar latitudes (Holdridge 1967, Sawyer and Lindsay 1963, Tosi 1964) (Fig. 2).

The hexagonal areas are termed life zones. When a specific site is located on the Holdridge model, a trinomial designation corresponding to its latitudinal position, altitudinal belt, and humidity province is applied. If the station lies in the basal al-

titudinal belt, the latitudinal region alone is used with the humidity province. An example will illustrate this procedure. Logan, Utah, lies at an elevation of 4,790 ft (1460 m), has a mean annual biotemperature of 10.0 C and a mean total annual precipitation of 16.64 inches (423 mm). Using the standard lapse rate of 6 C per thousand meters, a mean annual sea level biotemperature of 18.76 C is calculated corresponding to the *subtropical* latitudinal region (Fig. 2). The actual biotemperature of 10.0 C corresponds to the *montane* altitudinal belt (Fig. 2). The lines for a 10.0 C biotemperature and 423 millimeters precipitation intersect within the *steppe* life zone (Fig. 1). The trinomial life zone designation of Logan, Utah, would be *subtropical montane steppe*.

The question is, do all communities of the world falling into a particular life zone, e.g., subtropical montane steppe, have similar values of C and can they be treated in the conservation sense in a similar way?



Note that we are aware that the evolution of species, major taxa differences, and the specific species-species interactions in the various examples of particular life zones will all dictate detailed differences from place to place. Despite this, the question remains—is there a least common denominator of similarity such that not every community in the world will have to be studied before it can be conserved? If ecological laws really exist this least common denominator should be identifiable at some level of resolution, albeit generalized.

The first step in answering the specific question at hand is to ascertain whether or not the Holdridge model is applicable simultaneously to plants and animals (communities), outside of the tropics and in an area where sufficient climatic and distribution data are available.

Since the few tests of the Holdridge model by people outside the Holdridge group

(see review Holdridge et al. 1971) suggest its plausibility for vegetation (Lindsey and Sawyer 1970, Sawyer and Lindsey 1963, 1971, Thompson 1966), tropical birds (Slud 1960, 1976), and tropical reptiles and amphibians (Heyer 1967), a more detailed faunal and vegetational test seems appropriate. We report here on an attempt to answer the question whether life zones predicted on Holdridge's model do coincide with the patterns of distribution of animals and plants in nature to a significant degree.

METHODS

Data from 68 weather stations, selected from throughout Utah and having long climatic records (i.e., a minimum of 30 year averages of monthly temperatures and annual precipitation based on 1931-1960 records) were the main data base to generate the "theoretical life zones" of Utah. Re-

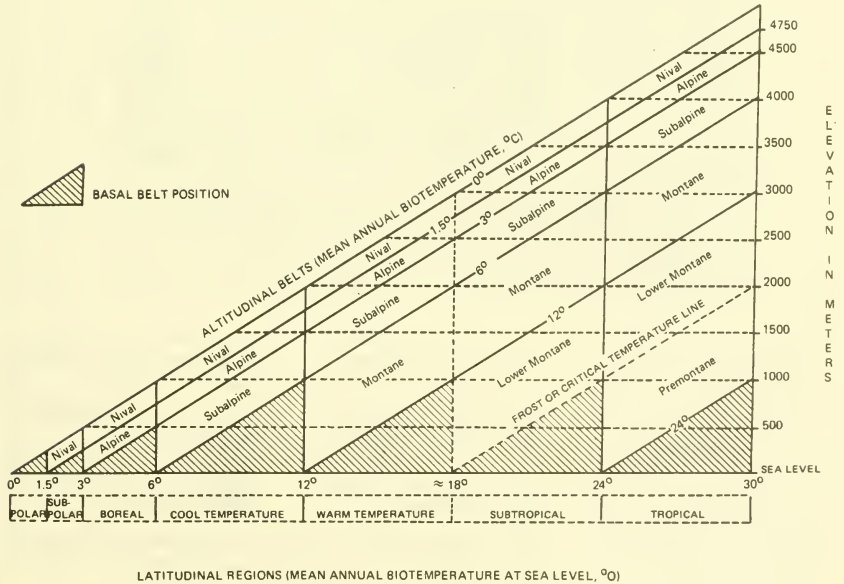


Fig. 2. Approximate guideline positions of latitudinal and altitudinal corrections to the Holdridge life zone system. Data based on an average adiabatic lapse rate of 6°C/1000 m (after Holdridge 1967).

cords of longer duration are available for certain stations. In these cases averages based on the total years of record are used.

Records of shorter duration are used wherever climatological data gaps occurred in critical geographic areas.



Subtropical Lower
Montane Desert Scrub

Subtropical Montane
Dry Scrub

Warm Temperate Montane
Moist Forest

Subtropical Lower
Montane Steppe

Subtropical Montane
Steppe

Warm Temperate Montane
Wet Forest

Subtropical Montane
Desert

Subtropical Montane
Moist Forest

Warm Temperate Subalpine
Moist Forest

Subtropical Montane
Desert Scrub

Subtropical Montane
Wet Forest

Warm Temperate Subalpine
Wet Forest

Fig. 3. Predicted potential life zone map of Utah. Assignment of localities to Holdridge life zones derived entirely from abiotic data based on United States Weather Bureau data corrected as described in the text.

Temperature and precipitation data provide only a rough approximation of the life zones because of topographic and physiognomic complexity. Maps of available heat, potential evapotranspiration, and normal annual precipitation from Jeppson et al. (1968) provided information to correct for these irregularities. Additionally, we had access to precipitation data from the United States Forest Service, Dixie National Forest, snow survey data from the Soil Conservation Service, and data reported in the literature (Price and Evans 1937). All of these data were used to derive estimates of values of the three factors necessary to define the hypothetical life zones of a particular locality.

The development of certain regression relationships (Figs. 9, 10) permitted us to take point data and derive yearly values and thus estimate life zone boundaries where few weather stations were available. This was particularly valuable because Utah weather stations are generally in the valleys. The station data or calculated points were plotted on a life zone chart (Fig. 1). Names were applied to life zones using the altitudinal and latitudinal corrections (Fig. 2). Life zone designations were then used to generate a theoretical life zone map (Fig. 3).

To determine whether or not the hypothetical life zones coincided with existing or potential life zones, several maps were generated or used.

The recent vegetation map of Cronquist et al. (1972), interpreted in light of Küchler's (1964) map, was used as the vegetation standard (Fig. 4). Additionally maps were prepared of conifer (Fig. 5) and some semiarid shrub (Fig. 6) distributions. Conifer distributions are taken from Little (1971). Shrub distributions are based on field data, unpublished dissertations, and analysis of herbarium specimens at Brigham Young University and Utah State University.

Maps of mammal biotic provinces (Fig. 7) were adapted from Durrant (1952), while a series of reptile and amphibian maps were

drawn (Fig. 8) based on data in Stebbins (1966). These two groups of vertebrates were used because they represent taxa of relatively high habitat fidelity, relatively low vagility (compared to birds), and well-known distributions, and they represent a range of physiologies (e.g., ectotherms vs. endotherms).

RESULTS AND DISCUSSION

The "hypothetical" life zone map derived entirely from estimates of abiotic factors according to the Holdridge (1967) scheme is presented in Fig. 3.

A comparison of Fig. 3 to the Utah vegetation map (Fig. 4) reveals interesting similarities and differences. The vegetation map is more detailed in the Great Basin desert (western one-half of the state) area and the Canyonlands floristic section (southeastern one-fourth) than the hypothetical map. In mountainous regions (Montane Zone, Fig. 4) the hypothetical map is more detailed. These differences are merely matters of scale in some cases and map basis in others. Much of the Great Basin desert mosaic is undoubtedly due to edaphic factors in the Cronquist et al. (1972) presentation. Since the vegetation map relies on species distributions, shadscale (*Atriplex confertifolia*) vs. sagebrush (*Artemisia tridentata*) communities are differentiated even though they may be in similar climate zones.

In the montane areas the Cronquist map, because of scale, recognizes one community while the hypothetical map includes topographically related climatic changes and predicts community differences. Similar reasoning explains the Canyonland area discrepancies between the two maps.

An integrated interpretation of the maps suggests a high degree of coincidence. The creosote bush vegetation zone clearly coincides with an isolated part of the Subtropical Lower Montane Desert Scrub. The Subtropical Montane Desert Scrub plus Subtropical Montane Steppe clearly coincides with the sagebrush plus shadscale vegetation

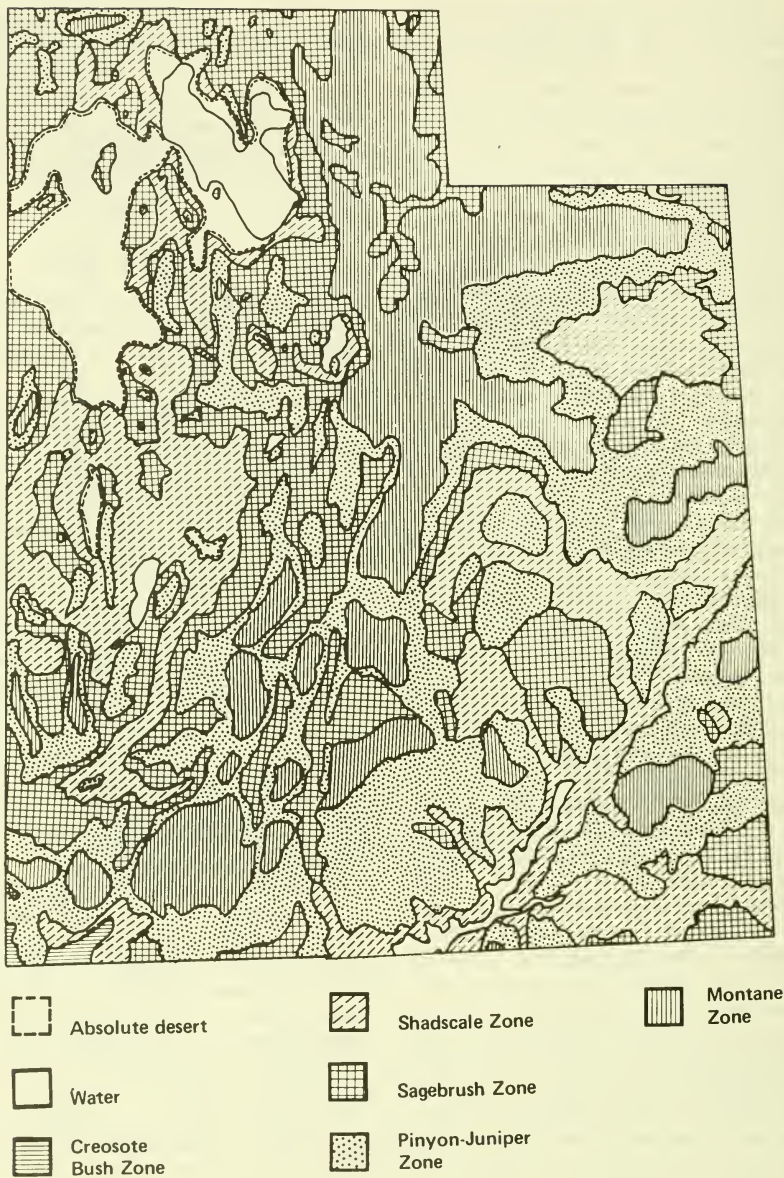


Fig. 4. Vegetation map of Utah redrawn from Cronquist et al. (1972) and modified slightly with reference to field notes and the map of Küchler (1964).

zones. The Canyonlands floristic section coincides well with large sections of the Subtropical Lower Montane Desert Scrub.

The Absolute Desert vegetation zone coincides with Subtropical Montane Desert.

Finally there is high overlap of the aggregated montane hypothetical life zones and the Montane vegetation zone.

Analysis of conifer distributions (Fig. 5), mainly montane forms, in conjunction with

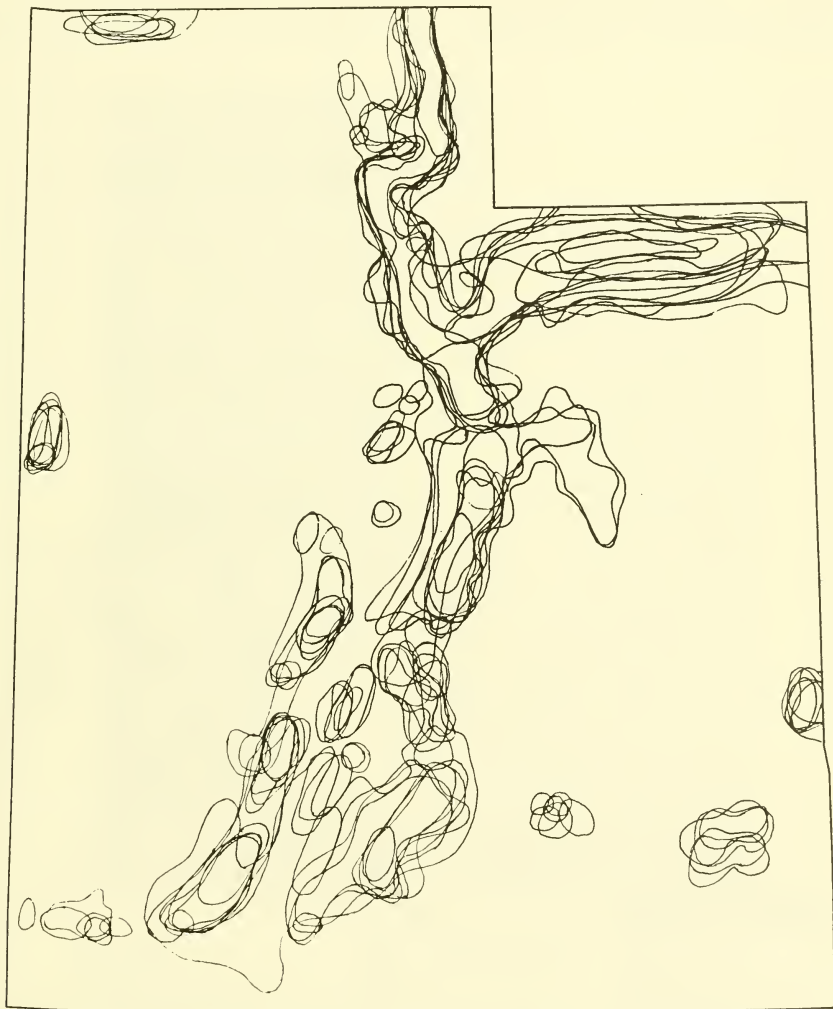


Fig. 5. Distribution outlines of 10 conifers in Utah (adapted from Little 1971). Species include *Abies concolor*, *A. lasiocarpa*, *Juniperus communis*, *J. scopulorum*, *Picea engelmannii*, *P. pungens*, *Pinus contorta*, *P. flexilis*, *P. ponderosa*, *Pseudotsuga menziesii*.

the hypothetical map (Fig. 3) shows surprisingly close fits of species boundaries and hypothetical life zone boundaries. This fit is biologically more meaningful than the rec-

ognition of a single montane vegetation for the purpose of predicting management practices. It is well known that steep topographic gradients cause community bound-

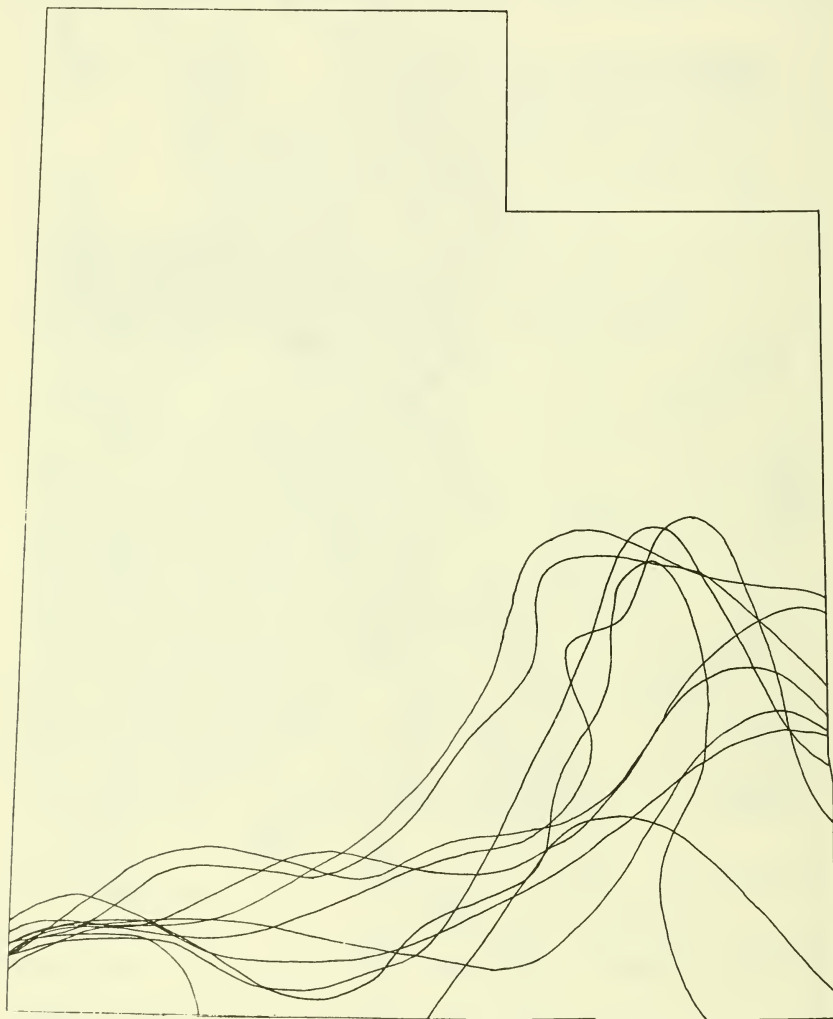


Fig. 6. The distribution limits of 13, mainly semiarid woody plants with limits in southern Utah. Data derived from unpublished theses, dissertations, and analysis of herbarium specimens and field notes. Species include: *Berberis fremontii*, *Encelia frutescens*, *Fraxinus anomala*, *Yucca angustissima*, *Yucca baccata*, *Lycium pallidum*, *L. torreyi*, *Coleogyne ramosissima*, *Quercus undulata*, *Dalea fremontii*, *D. lanata*, *D. polyadenia*, and *D. thompsonae*.

aries to become discrete when they otherwise form continua (Beals 1969). The vegetation map is generalized beyond management usefulness in the area of mountains.

The non-Great Basin desert semiarid woody plants mapped (Fig. 6) approximate the distribution of the Subtropical Lower

Montane Steppe plus Subtropical Lower Montane Desert Scrub hypothetical life zones. The Mojave desert section of Utah (extreme southwestern corner) is not differentiated in the hypothetical map from the larger Canyonlands area of Subtropical Lower Montane Desert Scrub.

Interestingly, the woody plant, mammal,

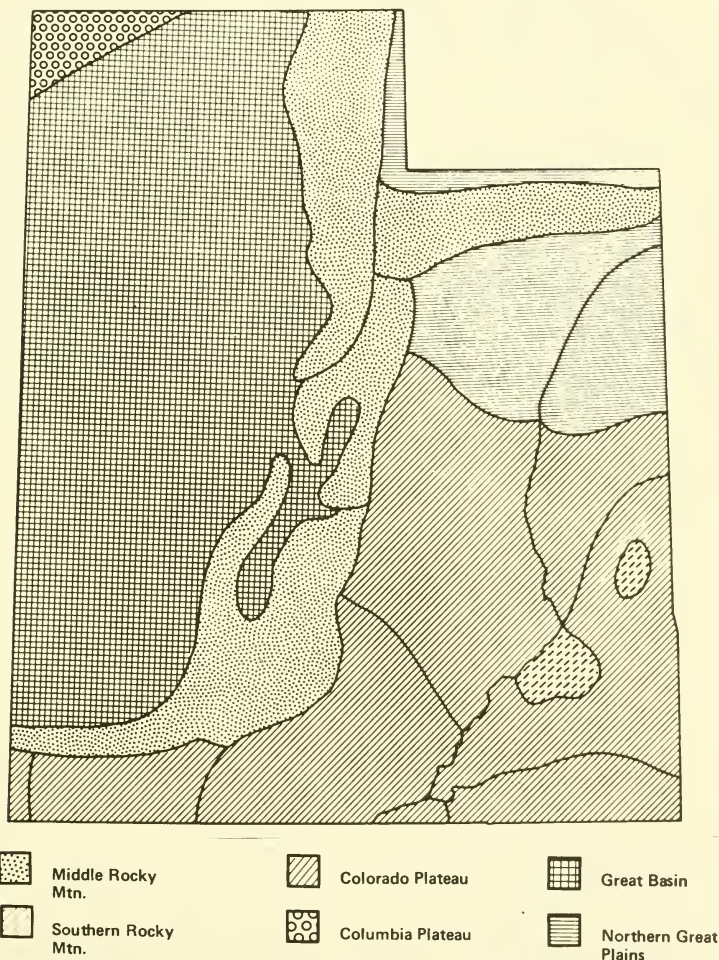


Fig. 7. Faunal areas of Utah based on mammal distributions. (Durrant 1952). Lines within a faunal area are boundaries of one of Durrant's provinces or subcenters.

reptile, and amphibian data (Figs. 6, 7, 8) suggest no absolute differences, but rather a gradual diminution of species numbers in the case of animals and replacement of shrub species. This is not to say that the use

of animal and plant species distributions cannot be used to delimit the Mojave desert. MacMahon (1977b) defines boundaries of all North American deserts based on exactly such data.

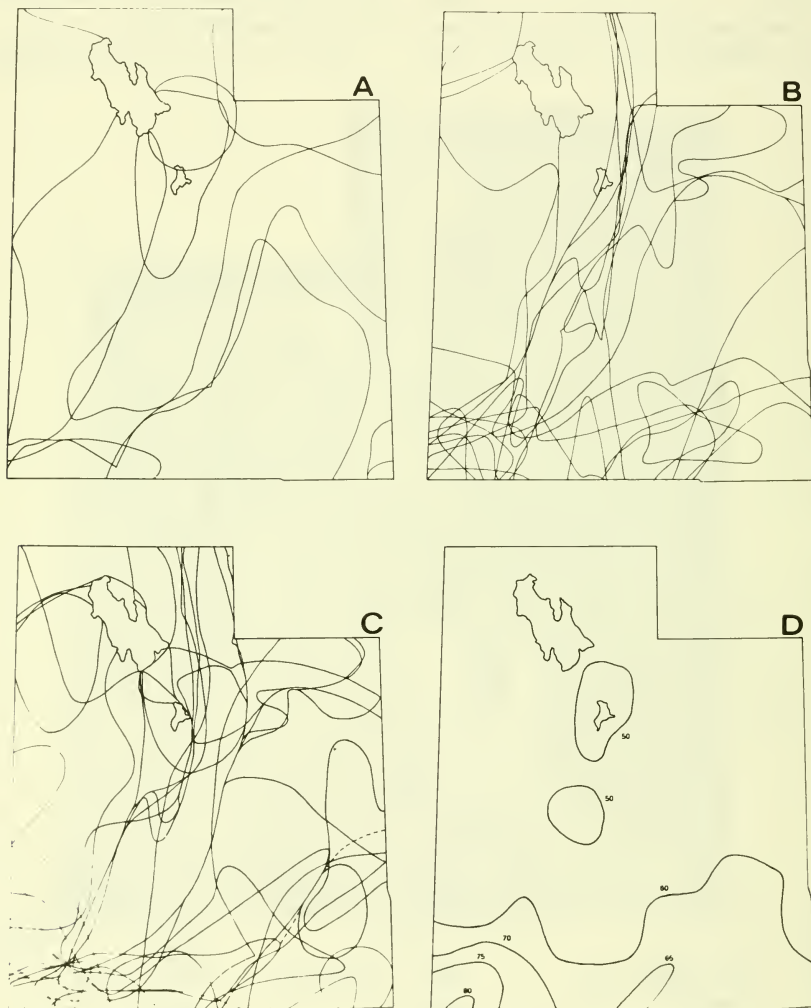


Fig. 8. Distribution limits of reptiles and amphibians in Utah based on Stebbins (1966). A-boundaries of amphibians. B-boundaries of lizards. C-boundaries of snakes. D-analysis of the percentage of the entire Utah herpetofauna occurring in any one area. Analysis based on a grid of 10 x 10 mi (16 x 16 km) cells.

The point is that one must pick certain species as indicators to rigidly define the Mojave desert, but an analysis of the distributions of all species in the desert communities shows gradual loss or replacement over a broader area. The same is true for the Great Basin desert. The gradual species shifts and assignment of indicators is detailed in MacMahon (1977b).

The Holdridge scheme separates the Great Basin desert from the other semiarid areas of the state by segregating western Utah into Subtropical Montane Desert Scrub plus Subtropical Montane Steppe. We believe this differentiation is probably important, because western Utah communities subjectively appear to us to be quite different from those of the southeast corner despite floral overlap. Thus the vegetation map implies a higher degree of similarity than we believe exists, particularly for management purposes. Again, animal boundaries (Figs. 7, 8) are strongly coincident with separation of the Canyonlands area from the western deserts.

All data suggest that the Holdridge

scheme effectively predicts plant- and animal-based life zone boundaries, if one can ignore a few "indicator" species. These data reinforce the general findings of others mentioned previously that the Holdridge scheme shows promise, but are more persuasive in that they use plants and animals in a topographically complex area where distributions are well known.

An interesting offshoot of these analyses are shown in Figures 9 and 10. It is usually assumed that long-term weather records would be necessary to derive Holdridge's climatic variables. Our data suggest, for Utah, that mean annual biotemperature can be predicted from mean annual temperature (Fig. 9). This is not surprising, but it means that one can take mean annual temperature data from a weather station in a valley corrected for altitude, etc., to get a corrected mean annual temperature for a place distant from that station. Mean biotemperature may be read directly from the curve or calculated from the formulae. Additionally, for Utah sites, a single measurement of snow accumulation on one day a year (1 April, Snow Water Equivalents) predicts annual precipitation (Fig. 10). For Utah this high

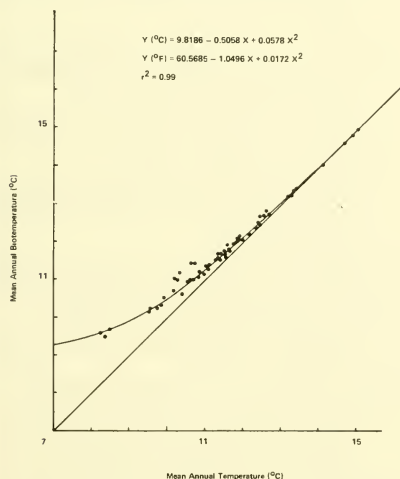


Fig. 9. Relationship between mean annual biotemperature and mean annual temperature for Utah weather stations.

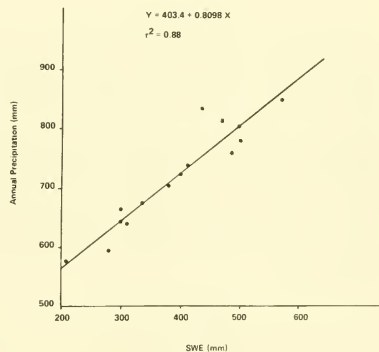


Fig. 10. Relationship between the 1 April snow water equivalent (SWE) and the annual precipitation for localities in the Manti-LaSal National Forest having snow courses studied by the United States Soil Conservation Service.

correlation is due in part to the high percentage of precipitation (60 percent or more) that comes as snowfall. A similar relationship may be of no value in other areas, but these results suggest that a person might be able to develop various other corrections specific to particular geographic areas. The prospect of using simple data extends the potential use of the Holdridge scheme. Additionally, since one only needs values for two variables to assign an area to a life zone hexagon, one may actually read the approximate value of the unknown third parameter off of the life zone model (Thompson 1966).

The Holdridge life zone model does predict plant and animal aggregations for Utah with reasonable accuracy. The next step to reach the final goal of using this scheme to portion the earth into a reasonable number of subsections for management purposes is to apply the scheme to another area containing organisms not closely related to those of Utah and then to determine whether or not a similar value of C obtains for the unrelated areas falling into the same life zone. That analysis must be left for another place and time.

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SUBJECT AND SPECIES INDICES FOR
INTERMOUNTAIN BIOGEOGRAPHY: A SYMPOSIUM

- Abajo Mountains, p. 61, 77.
Albion Mountains, p. 83.
Allopatric ranges, p. 71, 150, 153, 201.
Alpine biota, p. 11, 67, 72, 105, 109, 112.
Altitude, p. 29, 245.
Amphibians, p. 43, 245.
Angiosperms, p. 5, 6, 7.
Annual plants, p. 85, 87, 115, 170.
Aquarius Plateau, p. 65.
Arctic, p. 11, 105, 111, 112.
Arcto-Tertiary flora, p. 8, 9, 10, 238.
Area, p. 90, 91, 122, 209, 220, 245.
Arizona, p. 4, 43, 68, 105.
Ash Meadows, p. 140.
Asia, p. 7, 8, 237.
Aspen forest, p. 137.
Australia, p. 8.
Barriers, p. 17, 20, 28, 29, 30, 31, 32, 38, 47, 61, 63, 66, 71, 83, 84, 88, 107, 121, 122, 152, 167, 197, 217.
Baseline data, p. 72.
Beartooth Mountains, p. 105, 110, 111.
Beaver Dam Mountains, p. 50, 58, 73.
Bees, p. 13.
Beringia, p. 10, 13, 237.
Biogeographic regions, p. 106, 115, 119, 120, 134, 137, 202, 245.
Biogeography, p., 158, 209, 245.
Biotemperature, p. 255.
Bird dispersed plants, p. 96, 97.
Birds, p. 5, 12, 55, 89, 98, 137, 209, 220.
Bison, p. 12.
Black Pine Mountains, p. 122.
Blue Lake, p. 101.
Body size, p. 68, 69, 99, 215, 221.
Boreal biota, p. 31, 55, 59, 63, 71, 77, 137, 157, 209.
Bryce Canyon National Park, p. 83, 88, 93.
Burbank Hills, p. 122.
Burro, p. 12.
California, p. 13, 43, 55, 56, 57, 82.
Camel, p. 12.
Canada, p., 11, 161.
Carnivores, p. 222.
Carson Range, p. 212.
Cassia Mountains, p. 83.
Center of distribution, p. 7, 8, 237.
Charleston Peak, p. 105.
Chemotaxonomy, p. 238.
Chihuahua, p. 46.
Chile, p. 8.
Circumboreal flora, p. 11.
Clark Mountain, p. 98.
Climate, p. 3, 85, 88, 99, 108, 119, 130, 134, 144, 197, 245.
Clinal variation, p. 55, 64, 65, 66, 67, 68.
Coahuila, p. 46.
Colonization, p. 17, 31.
Color, p. 68.
Colorado, p. 4, 6, 44, 56, 57, 67, 68.
Colorado Plateau, p. 4, 43, 47, 57, 192, 198, 206, 255.
Colorado River, p. 17, 20, 27, 31, 33, 34, 38, 67, 139, 140.
Community structure, p. 141.
Competition, p. 37, 129, 152.
Confusion Range, p. 122.
Coniferous forest, p. 11, 137, 147, 221.
Continental climate, p. 3, 4, 7, 99.
Continental drift, p. 4, 18.
Craters of the Moon, p. 5.
Cretaceous, p. 4, 5, 6, 7, 9, 12, 105.
Death Valley, p. 20, 26, 32.
Deciduous trees, p. 8.
Deep Creek Mountains, p. 61, 65, 68, 72, 73, 77, 83, 92, 93, 111, 212.
Desatoya Range, p. 212.
Diamond Mountains, p. 212.
Dicotyledons, p. 6, 7.
Dinosaurs, p. 12.
Diptera, p. 13.
Disjunct ranges, p. 44, 81, 147, 153, 237.
Dispersal, p. 5, 17, 27, 71, 81, 93, 94, 96, 98, 111, 197, 199, 212.
Distance, p. 89, 90, 91, 93, 114, 200, 209.
Drainage basins, p. 18, 19, 20, 21.
East Humboldt Mountains, p. 108, 122, 133.
East Tintic Mountains, p. 83, 93.
Ecological role, p. 141.
Edaphic factors, p. 10, 89, 99, 109, 110,

- 115, 116, 161, 164, 191, 197, 205, 207.
Elephant, p. 12.
Elevation, p. 11, 83, 85, 89, 90, 91, 122, 126, 220.
Elk Ridge, p. 61.
Elko, p. 140.
Ely, p. 140.
Endangered species, p. 24, 25, 37, 72.
Endemics, p. 13, 17, 22, 35, 36, 43, 55, 57, 81, 87, 91, 97, 105, 110, 111, 113, 171, 192, 204, 229.
Eocene, p. 4, 5, 6, 7, 12, 18.
Eurasia, p. 7, 8, 9, 12.
Europe, p. 13.
Evolution, p. 3, 8, 13, 36, 115, 161, 170, 229, 238.
Excelsior Mountains, p. 122.
Extinct species, p. 22, 24, 25, 98, 217, 221.
Extinction, p. 3, 12, 13, 17, 28, 31, 32, 37, 39, 73, 98, 99, 209.
Fauna, p. 3.
Fidelity index, p. 199.
Fish, p. 17, 210, 223.
Fleshy fruits, p. 84, 94, 96.
Flora, p. 3, 81, 86.
Forbs, p. 96.
Fossils, p. 17, 25, 26, 28, 44, 55, 56, 166.
Frenchman Flat, p. 43.
Frisco Mountains, p. 61, 77.
Geologic history, p. 3, 4, 71.
Glaciers, p. 10, 20, 44, 69, 71, 106, 108, 161, 192.
Gondwanaland, p. 6, 9, 13.
Goose Creek Mountains, p. 122.
Goose Lake, p. 20, 33, 34.
Graminoides, p. 87, 96.
Grand Canyon, p. 17, 33.
Grant Range, p. 212.
Grasses, p. 3, 87, 96.
Grassland, p. 10, 73, 170.
Great Basin, p. 3, 17, 19, 43, 45, 47, 49, 55, 57, 81, 119, 198, 209, 255.
Great Plains, p. 44, 55.
Great Salt Lake, p. 55.
Green River, p. 27.
Green River flora, p. 6.
Gymnosperms, p. 5.
Habitat diversity, p. 59, 63, 89, 119, 122, 125, 147, 197, 209, 215, 220.
Harney Basin, p. 34.
Henry Mountains, p. 61, 77.
Herbaceous plants, p. 3, 7, 8, 98, 170.
Herbivores, p. 222.
Highland Mountains, p. 122.
Holdridge's Life Zones, p. 245, 246, 247.
Horse, p. 12.
House Range, p. 61, 77.
Humboldt River, p. 139, 140.
Hybridization, p. 8, 10, 11, 55, 58, 69, 153, 156, 161, 241.
Hymenoptera, p. 13.
Hypsithermal (Altitheal) period, p. 11, 20, 109, 111, 129, 167.
Idaho, p. 4, 43, 44, 56, 82, 140.
Immigration, p. 209.
Independence Mountains, p. 108.
Insects, p. 13.
Intercalary meristem, p. 12.
Introductions, p. 17, 37, 39, 72, 98.
"Islands," p. 5, 17, 55, 59, 72, 73, 81, 82, 88, 90, 105, 106, 161, 209.
Jarbidge Mountains, p. 72, 83, 97, 108, 115.
Jemez Mountains, p. 44.
Jurassic, p. 5, 12, 13.
Kaibab Plateau, p. 83.
Karyotype, p. 161, 229, 230, 231, 238.
Kawich, p. 140.
Klamath River, p. 17, 20, 26, 33, 34.
Lake Bonneville, p. 20, 26, 32, 34, 71, 161.
Lake Idaho, p. 19, 24.
Lake Lahontan, p. 20, 26, 32, 34, 55, 71, 131, 161.
La Sal Mountains, p. 61, 77.
Lassen Volcanic National Park, p. 83.
Latitudinal effects, p. 126, 137, 142.
Laurasia, p. 6, 9, 13.
Lava, p. 4.
Lifeform of plants, p. 84, 87.
Longevity, p. 99.
Longitudinal effects, p. 126.
Madro-Tertiary flora, p. 8, 9, 10.
Mainlands (continents), p. 88, 90, 121, 215.
Mammals, p. 5, 11, 31, 55, 62, 89, 98, 209, 220, 245.
Management, p. 1, 2, 17, 39, 53, 72, 100, 101, 134, 229, 230, 239, 245.
Markagunt Plateau, p. 65.
Meadow Valley Wash, p. 38, 58, 139, 140.

- Mediterranean region, p. 8.
Merriam effect, p. 129.
Mexico, p. 7, 8, 9, 43, 46, 161.
Mineral Mountains, p. 61, 77, 122.
Miocene, p. 3, 4, 7, 10, 12.
Mojave biota, p. 202.
Mojave Desert, p. 7, 13, 38, 55, 58, 105, 125, 253.
Molluscs, p. 55.
Monitor Range, p. 122, 133.
Monocotyledons, p. 7.
Montana, p. 7, 68.
Montane biota, p. 11, 63, 203, 212.
Mount Timpanogos, p. 83, 93.
Nature reserves, p. 245.
Navajo Mountains, p. 61, 77.
Needle Range, p. 61, 77, 122.
Nevada, p. 4, 18, 43, 45, 55, 56, 65, 67.
New Mexico, p. 4, 43, 44, 68.
New World, p. 9.
Niche breadth, p. 28, 61, 96, 100, 200, 207, 222.
Normalizing selection, p. 201.
North America, p. 7, 8, 9, 12.
Oak woodland, p. 10, 11, 129, 137.
Olancho Peak, p. 105, 111.
Old World, p. 7, 8.
Oligocene, p. 4, 6, 7, 18, 105.
Oquirrh Mountains, p. 61, 65, 66, 68, 77, 212.
Oregon, p. 33, 34.
Overgrazing, p. 53.
Overkill, p. 3.
Owens River, p. 20, 26, 32.
Pack rat middens, p. 43.
Pahranagat, p. 140.
Pahrump, p. 140.
Paleocene, p. 6, 7, 105.
Palm, p. 5, 6.
Panamint Range, p. 212.
Parasites, p. 99.
Paunsaugunt Plateau, p. 65, 212.
Pavant Mountains, p. 65.
Permian, p. 13, 105.
Physiological adaptations, p. 116.
Phytogeography, p. 105.
Pilot Peak, p. 122, 212.
Pine Forest Mountains, p. 97, 101.
Pine Valley Mountains, p. 61, 77, 83, 93, 122, 198.
Pinyon-juniper woodland, p. 10, 43, 55, 57, 73, 100, 119, 137, 142, 213.
Pit River, p. 17.
Plant succession, p. 133.
Pleistocene, p. 3, 12, 44, 48, 55, 63, 71, 81, 221, 223.
Pleistocene pluvials, p. 17, 19, 43, 105.
Pliocene, p. 4, 7, 17, 38, 105.
Pluvials, p. 31, 71, 166.
Pollen record, p. 5, 240.
Pollinating insects, p. 3, 13.
Polyploidy, p. 10, 109, 240.
Population size, p. 221.
Precipitation, p. 255.
Precipitation/evaporation ratio, p. 5, 10, 11, 28, 31, 71.
Predation, p. 37.
Primitive man, p. 3, 55.
Pyramid Lake, p. 55.
Quaternary, p. 56, 170.
Raft River Mountains, p. 61, 67, 68, 77, 83.
Range limits, p. 197.
Red Butte Canyon, p. 83, 93.
Refugia, p. 43, 48, 115.
Reptiles, p. 43, 245.
Riparian woodland, p. 137, 147, 205.
Roberts Creek Mountains, p. 212.
Rocky Mountains, p. 4, 11, 13, 17, 55, 99, 105, 108, 215.
Ruby Mountains, p. 20, 33, 72, 83, 87, 92, 93, 97, 105, 108, 110, 111, 115, 133, 212.
Sacramento Mountains, p. 44.
Sagebrush steppe, p. 55, 56, 73, 129.
Sagehen Creek, p. 83.
San Francisco Peak, p. 105, 108, 111, 113, 115.
Santa Rosa Mountains, p. 83, 97, 108.
Saprophytes, p. 99.
Schell Creek Mountains, p. 122, 212.
Sequoia-Kings Canyon National Park, p. 83.
Sevier River, p. 53.
Sheep Mountains, p. 212.
Shoshone Mountains, p. 122.
Shrubs, p. 8, 87, 96, 170, 229.
Sierra Nevada Mountains, p. 4, 17, 31, 55, 57, 67, 81, 96, 99, 105, 108, 111, 212, 215.
Silene acaulis, p. 110, 112.

- Similarity indices, p. 17, 21, 26, 27, 95, 105, 113.
- Snake Range, p. 72, 109, 212.
- Snake River, p. 17, 20, 26, 31, 32, 33, 139.
- Snake River Plain, p. 4, 17, 18, 38, 44.
- Sonora, p. 46.
- Source areas, p. 81, 90, 91, 92, 93, 115, 141, 164.
- South Africa, p. 8.
- South America, p. 8, 9, 12.
- Southwest, p. 57.
- Speciation, p. 138, 152.
- Species-area curves, p. 17, 31 61, 81 88, 97, 122, 215, 245.
- Species diversity, p. 31, 37, 56, 59, 81, 82, 87, 96, 101, 105, 122, 124, 125, 138, 139, 144, 220.
- Species equilibrium, p. 37, 81, 98, 99, 134, 209, 211.
- Spring Range, p. 83, 87, 91, 108, 111, 212.
- Spruce Mountain, p. 133, 212.
- Stansbury Mountains, p. 61, 77, 212.
- Sticktights, p. 84, 94, 96.
- Stream Capture, p. 27.
- Subalpine biota, p. 67.
- Sulphur Springs Range, p. 133.
- Sympatric species, p. 36, 71, 150, 153.
- Synecology, p. 119.
- Tavaputs Plateau, p. 65.
- Temperature inversions, p. 119, 131.
- Tertiary, p. 4, 6, 7, 8, 9, 12.
- Teton Mountains, p. 81.
- Therapsid reptiles, p. 12.
- Threatened species, p. 17, 23, 25.
- Timberline, p. 11, 106.
- Toana Mountains, p. 122.
- Toiyabe Mountains, p. 83, 87, 93, 108, 110, 111, 122, 133, 140, 212.
- Toquima Range, p. 110, 212.
- Transition zone, p. 197.
- Trees, p. 7, 87, 96, 99.
- Triassic, p. 12, 105.
- Trophic dynamics, p. 81.
- Truckee River, p. 140.
- Turnover rates, p. 223.
- Turtle Range, p. 98.
- Tushar Mountains, p. 65, 67, 122.
- Uinta Mountains, p. 44, 61, 64, 66, 68, 83, 212.
- Ungulates, p. 12.
- Utah, p. 4, 6, 43, 50, 51, 55, 56, 67, 82, 245.
- Utah Lake, p. 31.
- Vagility, p. 209, 223.
- Vegetation, p. 3, 72, 81, 119, 245.
- Vicariant species, p. 17, 27, 36.
- Virgin River, p. 33, 38, 47, 58, 68, 198.
- Volcanic activity, p. 17, 18.
- Vulnerable species, p. 17, 23, 24, 25.
- Wah Wah Mountains, p. 61, 77.
- Warner Mountains, p. 71, 83.
- Wasatch Mountains, p. 4, 17, 19, 31, 38, 44, 55, 61, 64, 66, 68, 77, 81, 83, 93, 96.
- Washington Co., Utah, p. 197.
- Wheeler Peak, p. 72, 83, 87, 93.
- White Mountains, p. 83, 108, 111, 113, 122, 212.
- White Pine Mountains, p. 212.
- White River, p. 33, 38.
- Wind dispersal, p. 84, 94, 96.
- Wyoming, p. 4, 43, 82.
- Yellowstone region, p. 18, 83.
- Yosemite National Park, p. 212.
- Z-values, p. 17, 31, 89, 209, 216.
- Zion Canyon, p. 58.
- Abies balsamea*, p. 11.
- Abies concolor*, p. 97, 98, 100, 148.
- Abies lasiocarpa*, p. 11, 86, 100.
- Accipiter cooperi*, p. 77.
- Accipiter gentilis*, p. 77.
- Accipiter striatus*, p. 77.
- Acer grandidentatum*, p. 86, 100.
- Acipenser transmontanus*, p. 22.
- Acipenseridae, p. 22.
- Aconitum columbianum*, p. 86.
- Acrocheilus alutaceus*, 23.
- Aegolius acadicus*, p. 77.
- Aeronautes saxatilis*, p. 77.
- Agastache pallidiflora*, p. 87.
- Agelaius phoeniceus*, p. 67.
- Agropyron pringlei*, p. 86.
- Agropyron spicatum*, p. 92.
- Allenrolfea*, p. 161.
- Allium*, p. 11, 86.
- Amelanchier alnifolia*, p. 92.
- Amelanchier utahensis*, p. 92.
- Androsace septentrionalis*, p. 112.

- Aneides hardyi*, p. 44.
Angelica scabrida, p. 87.
Antennaria marginata, p. 87.
Antennaria rosea, p. 111.
Antennaria soliceps, p. 87.
 Anthemidae, p. 7.
Anthus spinoletta, p. 79.
Aphelecora caerulea, p. 66.
Aphelecora coerulescens, p. 158.
Aplodontia rufa, p. 225.
Aquila chrysaetos, p. 77.
Aquilegia triternata, p. 87.
Archilochus alexandri, p. 78, 140.
Archoplites, p. 26.
Arctium, p. 85.
Arctostaphylos patula, p. 94.
Arenaria, p. 11.
Arenaria confusa, p. 87.
Arizona elegans, p. 48.
Artemisia, p. 7, 229.
Artemisia arbuscula, p. 92.
Artemisia douglasiana, p. 86.
Artemisia (section *Seriphidium*), p. 229.
Artemisia (section *Tridentatae*), p. 229.
Artemisia argilosa, p. 235.
Artemisia bigelovii, p. 233, 238, 241.
Artemisia cana, p. 235, 239.
Artemisia junceus, p. 237.
Artemisia leucodes, p. 237.
Artemisia longiloba, p. 235.
Artemisia maritima, p. 237.
Artemisia mendozana, p. 237.
Artemisia nova, p. 239.
Artemisia palmeri, p. 237, 239.
Artemisia pygmaea, p. 233.
Artemisia rigida, p. 233.
Artemisia rothrockii, p. 235.
Artemisia santonicum, p. 241.
Artemisia tridentata, p. 7, 92, 100, 235, 239, 249.
Asio otus, p. 77.
 Asteraceae, p. 7.
 Asteraeae, p. 7, 8.
Astragalus, p. 10.
Atriplex, p. 8, 161.
Atriplex acanthocarpa, p. 164.
Atriplex canescens, p. 161, 163, 164, 241.
Atriplex confertifolia, p. 161, 163, 249.
Atriplex corrugata, p. 161, 164.
Atriplex cuneata, p. 161, 163.
Atriplex falcata, p. 163.
Atriplex gardneri, p. 161, 164.
Atriplex garretti, p. 162, 164.
Atriplex hymenelytra, p. 164.
Atriplex navajoensis, p. 162.
Atriplex obovata, p. 161, 164.
Atriplex polycarpa, p. 164.
Atriplex torreyi, p. 164.
Atriplex tridentata, p. 162.
Balsamorhiza, p. 7, 86.
Balsamorhiza macrophylla, p. 86.
Balsamorhiza sagittata, p. 86.
Bidens, p. 85.
Bonasa umbellus, p. 77.
 Boraginaceae, p. 8.
 Brassicaceae, p. 8.
Bromus anomalus, p. 93.
Bromus breviaristatus, p. 86.
Bubo virginianus, p. 66, 77.
Bufo boreas, p. 49, 50, 51.
Bufo microscaphus, p. 45.
Bufo punctatus, p. 45.
Bufo woodhousei, p. 45.
Buteo jamaicensis, p. 66, 77.
Calamagrostis scopulorum, p. 86.
Callisaurus draconoides, p. 46.
Caltha leptosepala, p. 93, 110.
Calyptidium umbellatum, p. 111.
 Cardamine, p. 8.
Carduelis pinus, p. 79.
Carex amplifolia, p. 86.
Carex aurea, p. 86.
Carex elynoides, p. 110.
Carex helleri, p. 111.
Carex lanuginosa, p. 86.
Carex pulvinata, p. 110.
Carex scopulorum, p. 110.
Carex tahoensis, p. 86.
Carpodacus cassinii, p. 79.
Castilleja clokeyi, p. 87.
Castilleja linoides, p. 87.
Castilleja viscidula, p. 87.
Catharus fuscescens, p. 79, 140.
Catharus ustulatus, p. 79, 140.
 Catostomidae, p. 22.
Catostomus ardens, p. 24, 36.
Catostomus catostomus, p. 24.
Catostomus clarki, p. 24, 36.

- Catostomus columbianus*, p. 24.
Catostomus discobolus, p. 24, 36.
Catostomus fumeiventris, p. 24, 36.
Catostomus insignis, p. 24.
Catostomus latipinnis, p. 24.
Catostomus luxatus, p. 25.
Catostomus macrocheilus, p. 24, 36.
Catostomus occidentalis, p. 24.
Catostomus platyhrynchus, p. 17, 25, 27.
Catostomus sp., p. 24.
Catostomus tahoensis, p. 24, 36.
Catostomus warnerensis, p. 24, 36.
Ceanothus martini, p. 86, 93.
Ceanothus velutinus, p. 93.
Centurus uropygialis, p. 140.
Ceratodes, p. 10, 161.
Certhia familiaris, p. 65, 78, 144, 148.
Chaenactis, p. 7.
Chamaebatiaria millefolium, p. 100.
Charina bottae, p. 49, 50, 51.
Chasmistes brevisrostris, p. 25, 33.
Chasmistes cirius, p. 25.
Chasmistes liorus, p. 25.
Chasmistes sp. p. 25.
Cheilanthes gracillima, p. 86.
Chenopodiaceae, p. 8, 161.
Chordeiles minor, p. 67.
Chlorocrambe hastata, p. 86.
Chorizanthe, p. 170.
Chrysothamnus, p. 10.
Circaea, p. 85.
Cirsium clokeyi, p. 87.
Clematis columbiana, p. 86.
Clethrionomys gapperi, p. 225.
Cnemidophorus tigris, p. 48.
Coccyzus americanus, p. 140.
Coccyzus erythrophthalmus, p. 140.
Colaptes auratus, p. 67, 140.
Colaptes cafer, p. 69.
Colaptes chrysoides, p. 67.
Coleogyne, p. 43.
Coleonyx variegatus, p. 46.
Coleoptera, p. 13.
Coluber constrictor, p. 49.
Columba fasciata, p. 77.
Contopus borealis, p. 78.
Contopus sordidulus, p. 78.
Corallorhiza, p. 99.
Cottidae, p. 22.
Cottus bairdii, p. 17, 25, 27, 29, 36.
Cottus beldingi, p. 25.
Cottus confusus, p. 25.
Cottus echinatus, p. 25, 36.
Cottus extensus, p. 25, 36.
Cottus greenei, p. 26.
Cottus klamathensis, p. 26.
Cottus leiopomus, p. 26.
Cottus pitensis, p. 26.
Cottus princeps, p. 26.
Cottus rhotheus, p. 26.
Cottus tenuis, p. 26.
Crenichthys baileyi, p. 25, 36.
Crenichthys nevadae, p. 25, 36.
Crotalus cerastes, p. 48, 50.
Crotalus michelli, p. 48, 50.
Crotalus scutulatus, p. 48, 50.
Crotaphytus wislizeni, p. 46.
Cryptantha, p. 8.
Cryptantha mohavensis, p. 86.
Cyanocitta stelleri, p. 66, 78, 144, 157.
Cycloloma atripticifolium, p. 162.
Cynopterus nivalis, p. 87.
Cyprinidae, p. 22.
Cyprinodon breviradis, p. 25, 36.
Cyprinodon diabolis, p. 25.
Cyprinodon nevadensis, p. 25.
Cyprinodon radiosus, p. 25.
Cyprinodontidae, p. 22.
Cystopteris fragilis, p. 112, 115.
Dedeckera, p. 170.
Delphinium occidentale, p. 93.
Dendragapus obscurus, p. 65, 77, 157.
Dendrocopos pubescens, p. 140, 149, 157.
Dendrocopos scalaris, p. 140.
Dendrocopos villosus, p. 140.
Dendroica coronata, p. 79.
Dendroica gracialis, p. 79, 148.
Deschampsia caespitosa, p. 110.
Dipsosaurus dorsalis, p. 46.
Dodecatheon jeffreyi, p. 111.
Draba, p. 110.
Draba arida, p. 87.
Draba lemmonii, p. 111.
Dryocopus pileatus, p. 78.
Dumetella carolinensis, p. 140.
Eleocharis montana, p. 87.
Empetrichthys latos, p. 25, 36.

- Empetrichthys merriami*, p. 25, 36.
Empidonax difficilis, p. 78, 147, 150, 157.
Empidonax hammondi, p. 78, 147, 150.
Empidonax minimus, p. 152.
Empidonax oberholseri, p. 78.
Enceliopsis, p. 7.
Epilobium angustifolium, p. 86.
Eremichthys acros, p. 23.
Eremophila alpestris, p. 67, 78.
Erigeron, p. 8, 11.
Erigeron peregrinus, p. 110.
Erigeron ursinus, p. 86.
Erigeron watsoni, p. 87.
Eriogoneae, p. 186.
Eriogonoideae, p. 170.
Eriogonum, p. 10, 11, 110, 170.
Eriogonum gracilipes, p. 110.
Eriogonum holmgrenii, p. 87.
Eriogonum kingii, p. 87.
Eriophyllum, p. 7.
Eumeces skiltonianus, p. 50.
Eutamias alpinus, p. 225.
Eutamias amoenus, p. 225.
Eutamias dorsalis, p. 100, 221, 225.
Eutamias panamintinus, p. 225.
Eutamias quadrimaculatus, p. 225.
Eutamias quadrivittatus, p. 225.
Eutamias speciosus, p. 225.
Eutamias townsendii, p. 225.
Eutamias umbrinus, p. 100, 221, 225.
Falco sparverius, p. 77, 140.
Festuca arizonica, p. 87.
Fritillaria atropurpurea, p. 86.
Fundulus spp., p. 25.
Gentiana, p. 11.
Geothlypis tohniei, p. 79.
Geothlypis trichas, p. 67.
Geranium fremontii, p. 93.
Geum macrophyllum, p. 86.
Geum rossii, p. 86, 110.
Gila alvordensis, p. 23, 36.
Gila atraria, p. 23, 36.
Gila bicolor, p. 17, 23, 27, 28, 33, 36.
Gila coerulea, p. 23.
Gila copei, p. 23.
Gila cypha, p. 23, 33.
Gila elegans, p. 23, 33.
Gilia, p. 8.
Gilmania, p. 170.
Glaucidium gnoma, p. 77.
Glaucomyis sabrinus, p. 225.
Glyceria elata, p. 86.
Goodmania, p. 170.
Copherus agassizi, p. 46.
Grazia, p. 161.
Guiraca caerulea, p. 140.
Hackelia floribunda, p. 86.
Haplopappus, p. 7, 10.
Harfordia, p. 170.
Heliantheae, p. 7, 10.
Hesperiphona vespertina, p. 148.
Hesperoleucus symmetricus, p. 23.
Hierochloë odorata, p. 86.
Holbrookia maculata, p. 47.
Hollisteria, p. 170.
Holodiscus dumosus, p. 93.
Hulsea, p. 11, 86.
Hulsea algida, p. 111.
Hydrophyllaceae, p. 8.
Hyla arenicolor, p. 45.
Hymenoxys, p. 11.
Icterus bullockii, p. 69.
Icterus cucullatus, p. 140.
Icterus galbula, p. 69, 140.
Icterus galbula, p. 140.
Iotichthys phlegethontis, p. 23.
Iridoprocne bicolor, p. 140.
Ivesia pygmaea, p. 111.
Junco caniceps, p. 70, 80, 157.
Junco hyemalis, p. 70, 80, 157.
Juniperus, p. 7, 85.
Juniperus osteosperma, p. 43, 93, 98, 119.
Kalmia polifolia, p. 94.
Koeleria cristata, p. 110.
Koenigia islandica, p. 112.
Lampetra lethophaga, p. 22.
Lampetra minima, p. 22.
Lampetra tridentata, p. 22.
Lampropeltis getulus, p. 48, 49.
La Rivers, I., p. 18, 22, 23.
Larrea, p. 4, 43.
Lastarria, p. 170.
Lathyrus pauciflorus, p. 93.
Ledum glandulosum, p. 94.
Lepidium, p. 8.
Lepidomeda albivallis, p. 24, 36.
Lepidomeda altivelis, p. 24, 36.

- Lepidomeda mollispinis*, p. 24, 36.
Leipidomeda nittata, p. 24.
Leptotyphlops humilis, p. 48.
Lepus americanus, p. 225.
Lepus townsendii, p. 221, 225.
Lesquerella, p. 8.
Leucosticte atrata, p. 79.
Leucosticte tephrocotis, p. 157.
Lewisia pygmaea, p. 111.
Lewisia rediviva, p. 93.
Libocedrus decurrens, p. 86.
Lithospermum, p. 8.
Lomatium, p. 11.
Lonicera involucrata, p. 86.
Loxia curvirostra, p. 79.
Lupinus breweri, p. 111.
Marmota flaviventris, p. 221, 225.
Martes americana, p. 225.
Masticophis flagellum, p. 48.
Melospiza melodia, p. 140.
Mertensia arizonica, p. 86.
Mertensia toyabensis, p. 87.
Microtus longicaudus, p. 221, 225.
Microtus richardsoni, p. 225.
Minulus torreyi, p. 86.
Moapa coriacea, p. 24.
Moldavica parviflora, p. 86.
Molothrus ater, p. 66.
Mucrona, p. 170.
Muhlenbergia wrightii, p. 87.
Mustela erminea, p. 221, 225.
Myadestes townsendi, p. 79.
Mylocheilus caurinus, p. 24.
Mylopharodon, p. 26.
Myosotis, p. 11.
Myoxocephalus, p. 26.
Nemacaulis, p. 170.
Neotoma cinerea, p. 221, 225.
Neotoma lepida, p. 43.
Nicotiana attenuata, p. 94.
Nucifraga columbiana, p. 78, 97, 98.
Ochotona princeps, p. 221, 224, 225.
Oenothera caespitosa, p. 93.
Oncorhynchus tshawytscha, p. 22.
Ophcodrys vernalis, p. 49.
Ophisaurus attenuatus, p. 44.
Opuntia charlestonensis, p. 87.
Oporonis tolmiei, p. 140.
Orobanche, p. 99.
Orthocarpus tolmiei, p. 86.
Orthodon, p. 26.
Oryzopsis kingii, p. 86.
Osmorhiza chilensis, p. 86.
Otus asio, p. 67, 140.
Otus flammeocolus, p. 77.
Oxyria digyna, p. 110, 111, 112, 115.
Oxytheca, p. 170.
Pachistima myrsinites, p. 93.
Parus atricapillus, p. 66, 78, 140.
Parus gambeli, p. 65, 78.
Passerella iliaca, p. 71, 140, 153.
Passerina amoena, p. 69.
Passerina cyanea, p. 69.
Pedicularis, p. 11.
Penstemon, p. 10, 11.
Penstemon keckii, p. 87.
Peraphyllum ramosissimum, p. 94.
Perisoreus canadensis, p. 78.
Petrochelidon pyrrhonota, p. 66.
Phacelia, p. 8.
Phainopepla nitens, p. 140.
Phenacomys intermedius, p. 225.
Pheucticus melanocephalus, p. 79.
Phippsia algida, p. 112.
Phlox caespitosa, p. 111.
Phlox covillei, p. 110.
Phlox longifolia, p. 93.
Phrynosoma douglassi, p. 50.
Physaria, p. 8.
Picea engelmannii, p. 11, 97, 100.
Picea glauca, p. 11.
Picea pungens, p. 11, 86, 100.
Picoides tridactylus, p. 78.
Picoides villosus, p. 66, 78.
Pinicola enucleator, p. 79.
Pinus albicaulis, p. 94, 97.
Pinus aristata, p. 94, 97, 98.
Pinus banksiana, p. 11.
Pinus contorta, p. 11.
Pinus edulis, p. 86, 97.
Pinus flexilis, p. 97, 98.
Pinus jefferyi, p. 86, 98.
Pinus longaeva, p. 109, 148.
Pinus monophylla, p. 98, 129.
Pinus ponderosa, p. 86, 94, 98, 100, 129, 148.
Pipilo aberti, p. 140.
Pipilo chlorura, p. 79.

- Pipilo erythrophthalmus*, p. 79.
Piranga ludoviciana, p. 79.
Piranga rubra, p. 140.
Plagiobothrys, p. 8.
Plagopterus argentissimus, p. 24.
Plethodon neomexicanus, p. 44.
Plethodontidae, p. 44.
Polemoniaceae, p. 8.
Polemonium eximium, p. 111.
Polygonaceae, p. 170.
Polygonum bistortoides, p. 110.
Polygonum lapathifolium, p. 98.
Polygonum minimum, p. 111.
Polygonum pensylvanicum, p. 98.
Polygonum viviparum, p. 112.
Pooecetes gramineus, p. 79.
Populus tremuloides, p. 86.
Populus trichocarpa, p. 86.
Potentilla beanii, p. 87.
Primula capillaris, p. 87.
Primula parryi, p. 86, 93.
Progne subis, p. 78.
Prosopium abyssicola, p. 23.
Prosopium gemmiferum, p. 23.
Prosopium prolixus, p. 23.
Prosopium spilonotus, p. 23.
Prosopium williamsoni, p. 17, 23, 27, 36.
Prunus emarginata, p. 86.
Pseudoacris triseriata, p. 49.
Pseudotsuga menziesii, p. 11, 100, 148.
Pterostegia, p. 186.
Pterostegia, p. 170.
Ptychocheilus lucius, p. 23.
Ptychocheilus oregonensis, p. 23, 33.
Purshia tridentata, p. 86.
Pyrocephalus rubinus, p. 140.
Quercus gambelii, p. 11, 86, 98, 100.
Quercus turbinella, p. 11.
Rana pretiosa, p. 49, 51.
Ranunculus, p. 11.
Ranunculus jovis, p. 93.
Regulus calendula, p. 79, 148.
Regulus satrapa, p. 79, 148.
Relictus solitarius, p. 24, 27.
Rhinichthys cataractae, p. 17, 24, 27.
Rhinichthys falcatus, p. 24.
Rhinichthys osculus, p. 17, 24, 27, 28, 36.
Rhinichthys sp., p. 24.
Rhiniocheilus lecontei, p. 53.
Ribes cercum, p. 86.
Ribes wolfii, p. 86.
Richardsonius balteatus, p. 17, 23, 27, 36.
Richardsonius egregius, p. 23, 36.
Rorripa, p. 8.
Rubus parviflorus, p. 94.
Salicornia, p. 161.
Salix arctica, p. 110, 112.
Salmo apache, p. 22.
Salmo clarki, p. 17, 22, 27, 28, 36.
Salmo gairdneri, p. 22.
Salmo sp., p. 22.
Salmoides, p. 22.
Salpinx obsoletus, p. 79.
Salsola, p. 161.
Salvadora hexedepis, p. 48.
Salvelinus malma, p. 22.
Sarcobatus, p. 161.
Saxifraga, p. 11.
Saxifraga cespitosa, p. 112, 115.
Saxifraga flagellaris, p. 112.
Sayornis nigricans, p. 140.
Scleroporus elongatus, p. 51.
Scleroporus graciosus, p. 50.
Scleroporus magister, p. 47.
Sedum rosea, p. 111.
Selaginella selaginoides, p. 87.
Selasphorus platycercus, p. 78, 157.
Senecio multilobatus, p. 10.
Senecio streptanthifolius, p. 10.
Sequoiadendron giganteum, p. 86.
Sialia currucoides, p. 79, 150.
Sialia mexicana, p. 79, 140, 150.
Sibbaldia procumbens, p. 110.
Silene clokeyi, p. 87.
Sitanion hystrix, p. 86.
Sitta canadensis, p. 78, 148.
Sitta carolinensis, p. 78.
Sitta pygmaea, p. 78.
Sonora semianulata, p. 48, 49.
Sorex lyelli, p. 225.
Sorex palustris, p. 221, 225.
Sorex tenellus, p. 221, 225.
Sorex townsendi, p. 225.
Sorex vagrans, p. 221, 225.
Spermophilus armatus, p. 225.
Spermophilus beldingi, p. 221, 225.
Spermophilus lateralis, p. 221, 225.
Sphyrapicus ruber, p. 144, 157.

- Sphyrapicus thyroideus*, p. 78, 147.
Sphyrapicus varius, p. 78, 147, 157.
Spinus pinus, p. 148.
Spizella passerina, p. 80.
Stanleya, p. 8.
Stellula calliope, p. 78.
Stenogonum, p. 170.
Stetophaga ruticilla, p. 140.
Stipa californica, p. 86.
Streptanthus, p. 8.
Strix occidentalis, p. 77.
Suaeda, p. 161.
Sylvilagus nuttallii, p. 221, 225.
Synthyris ranunculina, p. 87.
Tachycineta bicolor, p. 78.
Tachycineta thalassina, p. 78.
Tamiasciurus douglasii, p. 225.
Tamiasciurus hudsonicus, p. 225.
Tanacetum compactum, p. 87.
Taxus brevifolia, p. 86.
Tegeticula, p. 3.
Thamnophis cyrtopsis, p. 48, 49.
Thalictrum fendleri, p. 86.
Thamnophis elegans, p. 49.
Thelypodium, p. 8.
Thermopsis montana, p. 86.
Thryomanes bewickii, p. 140.
Toxostoma dorsale, p. 140.
Trifolium andersonii, p. 86.
Trifolium monoense, p. 110.
Trisetum spicatum, p. 110, 112, 115.
Troglodytes aedon, p. 78, 140.
Tsuga mertensiana, p. 86.
Turdus migatorius, p. 79, 140.
Tyrannus tyrannus, p. 140.
Tyrannus verticalis, p. 140.
Urosaurus ornata, p. 47.
Uta stansburiana, p. 47.
Valeriana occidentalis, p. 93.
Vermivora celata, p. 79, 140, 157.
Vermivora luciae, p. 140.
Vermivora ruficapilla, p. 157.
Vermivora virginiae, p. 79, 157.
Viguiera, p. 7.
Viola adunca, p. 86.
Vireo bellii, p. 140.
Vireo gilvus, p. 79, 140.
Vireo olivaceus, p. 140.
Vireo solitarius, p. 79, 157.
Wilsonia pusilla, p. 79, 157.
Wyethia, p. 7.
Xanthium, p. 85.
Xyrauchen texanus, p. 25, 33.
Yucca, p. 3.
Zapus princeps, p. 225.
Zenaida asiatica, p. 140.
Zonotrichia iliaca, p. 80.
Zonotrichia leucophrys, p. 80.
Zonotrichia lincolni, p. 80.
Zonotrichia melodia, p. 66, 67, 80.

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